Biodiversity Conservation in Arid Environments Under Climate Change

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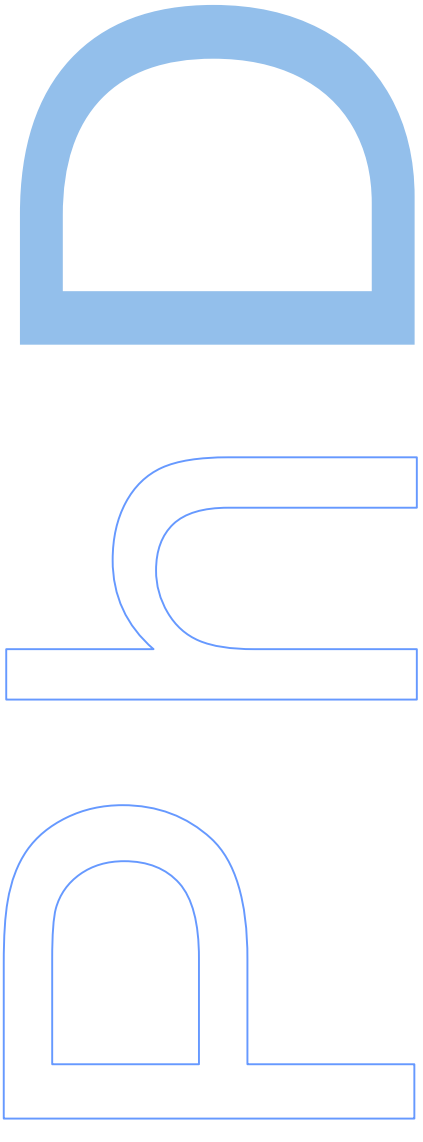

NOTA PRÉVIA

Na elaboração desta tese, e nos termos do número 2 do Artigo 4o do Regulamento Geral dos Terceiros Ciclos de Estudos da Universidade do Porto e do Artigo 31º do D.L. 74/2006, de 24 de Março, com a nova redação introduzida pelo D.L. 230/2009, de 14 de Setembro, foi efetuado o aproveitamento total de um conjunto coerente de trabalhos de investigação já publicados ou submetidos para publicação em revistas internacionais indexadas e com arbitragem científica, os quais integram alguns dos capítulos da presente tese. Tendo em conta que os referidos trabalhos foram realizados com a colaboração de outros autores, o candidato esclarece que, em todos eles, participou ativamente na sua conceção, na obtenção, análise e discussão de resultados, bem como na elaboração da sua forma publicada.

Este trabalho foi apoiado pela Fundação para a Ciência e Tecnologia (FCT) através da atribuição da bolsa de doutoramento (SFRH/BD/72522/2010).

To the memory of my father.

To my mother and grandmother.

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RESUMO

Os efeitos sinergéticos das actividades humanas e das alterações climáticas culminaram na actual crise de biodiversidade. O maior objectivo da Conservação da Biodiversidade é travar a perda de biodiversidade, através da definição de áreas prioritárias para a conservação que maximizem a representação das espécies e permitam a sua persistência. Os ambientes áridos são áreas negligenciadas mas importantes para a conservação onde os objectivos de representatividade e persistência podem ser atingidos enquanto o uso sustentável dos recursos é promovido. Esta tese contribui para a conservação da biodiversidade sugerindo medidas para identificar áreas adequadas e melhorando o conhecimento actual sobre os padrões de biodiversidade em ambientes áridos, particularmente no Saara- Sahel.

O principal objectivo da tese é abordar a conservação da biodiversidade em ambientes áridos, focando-se no Saara- Sahel, uma região onde a biodiversidade está sob forte controle climático e é vulnerável às alterações. Foram definidos quatro objectivos específicos: 1) comparar o desempenho de modelos de nicho ecológico construídos a diferentes escalas para prever a distribuição das espécies em áreas marginais e a distribuição de espécies ecologicamente plásticas; 2) avaliar o estatuto de conservação de espécies restritas às montanhas; 3) identificar *hotspots* locais de biodiversidade; e 4) identificar grupos funcionais vulneráveis às alterações climáticas futuras.

Foram analisadas as implicações associadas à selecção da extensão da área de estudo, da resolução e do valor de corte no desempenho de modelos de nicho ecológico para prever a distribuição de espécies em áreas marginais de ocorrência. Adicionalmente, os efeitos relacionados com a escala foram avaliados para espécies ecologicamente plásticas. Para planeamentos locais de conservação, sob as condições actuais, os modelos regionais com elevada resolução devem ser usados, uma vez que foram mais precisos em prever a actual distribuição de espécies em áreas marginais localizadas em zonas de transição abrupta, e na definição de áreas adequadas para a ocorrência de espécies plásticas. Valores de corte conservadores aplicados a modelos regionais melhoram a definição de áreas adequadas, o que permite identificar áreas a proteger no limite da distribuição das espécies.
Para avaliar estatutos de conservação, modelos de nicho ecológico foram aplicados na identificação de factores ambientais relacionados com a distribuição e de áreas

adequadas para espécies endémicas do Saara- Sahel (*Felovia vae* e *Agama boulengeri*). As áreas adequadas obtidas foram utilizadas para calcular o número de subpopulações, a extensão da ocorrência e da área de ocupação. Ambas as espécies estavam principalmente relacionadas coma ocorrência de lagoas rochosas, desertos rochosos e áreas nuas associadas às montanhas da Mauritânia, sendo consideradas "Pouco preocupantes". Estes estudos contribuíram para aumentar o conhecimento sobre espécies endémicas do Saara-Sahel e para salientar o valor biológico das montanhas da Mauritânia, como montanhas-ilha.

Para explorar a importância de lagoas rochosas de montanha (localmente conhecidas como *gueltas*) como *hotspots* locais da biodiversidade, o número de vertebrados total e de endémicos presentes em 69 gueltas foi quantificado e comparado com o número de espécies presentes nas áreas limítrofes e registadas na Mauritânia. Os gueltas foram classificados de acordo com a sua prioridade para a conservação, tendo em conta a percentagem de espécies endémicas e ameaças. Os gueltas constituem *hotspots* locais de biodiversidade, dado que são lugares minúsculos que albergam um número elevado de espécies, incluindo endémicas e são vulneráveis a secas e às actividades humanas. Dado que podem constituir refúgio perante futuros cenários de mudanças climáticas, são cruciais para a conservação a longo prazo da biodiversidade do Saara-Sahel e também para as comunidades locais, cuja economia é baseada na exploração da água e dos habitats produtivos limítrofes dos gueltas.

A estratégia funcional das espécies endémicas do Saara- Sahel foi resumida em grupos funcionais e a sua exposição à magnitude e velocidade da mudança climática foi avaliada com o objectivo de identificar os grupos funcionais mais vulneráveis às alterações climáticas. Sete grupos funcionais com diferentes níveis de vulnerabilidade à velocidade e magnitude das alterações climática foram identificados tendo em conta a sua distribuição actual. Os grupos funcionais constituídos por espécies adaptadas a ambientes áridos, com baixa capacidade de adaptação e dispersão, e que vivem em planícies foram identificados como sendo os grupos mais vulneráveis face às alterações climáticas. Este estudo dá indicações sobre a vulnerabilidade funcional face às alterações climáticas noutros desertos quentes do mundo.

Este trabalho contribuiu, através da combinação diferentes metodologias aplicadas a diferentes componentes da biodiversidade, para o aumento do conhecimento sobre os padrões de distribuição da biodiversidade e respectivas vulnerabilidades em ambientes áridos, que em última análise podem ser usados para a elaboração de programas sistemáticos de conservação.

PALAVRAS-CHAVE: alterações climáticas; ambientes áridos; conservação da biodiversidade; endémicas; estatuto de conservação; grupos funcionais; *hotspots* locais; lagoas rochosas; modelos de nicho ecológico; montanhas; Saara; Sahel.

SUMMARY

The synergetic effects of human activities and climate change come in the current biodiversity crisis. The major aim of Biodiversity Conservation is to halt biodiversity loss by defining priority areas for conservation that maximize species representation and enable persistence. The overlooked arid environments are important areas for conservation where the goals of representativeness and persistence can be achieved while promoting sustainable resource use. This thesis contributes to biodiversity conservation by suggesting good practices to accurate identify suitable areas and by improving current knowledge on biodiversity patterns in arid environments, particularly the Sahara-Sahel.

The main objective of the thesis is to address biodiversity conservation in arid environments, focusing on the Sahara-Sahel, a region where biodiversity is under strong climatic control and is vulnerable to climate change. Four specific goals were defined: 1) compare the performance of ecological niche models built at different scales to predict species distribution at range margins and the distribution of ecologically plastic species; 2) evaluate the conservation status of mountain restricted species; 3) identify local hotspots of biodiversity; and 4) identify functional groups vulnerable to future climate change.

The implications of the study area extent, resolution and threshold selection in the performance of ecological niche models to predict species distributions at range margins were analysed. Additionally, scale-related effects were assessed for ecologically plastic species. For local conservation planning under present conditions, fine-resolution regional models should be used, as they were more accurate in predicting current species distributions at range margins located in abrupt transition zones, and in defining suitable areas for the occurrence of ecologically plastic species. Conservative thresholds applied to regional models improve the definition of suitable areas to effectively design protected areas at the edge of species distributions.

Ecological niche models were applied to predict environmental factors related with species distributions and identify suitable areas for Sahara-Sahel endemic species (*Felovia vae* and *Agama boulengeri*), to ultimately evaluate their conservation status. Predicted suitable areas were used to calculate the number of subpopulations, the extent of occurrence and area of occupancy. Both species were mostly related with

rock-pools, rocky deserts and bare areas, and associated to Mauritanian mountains, being deemed as Least Concern. These studies contributed to increase knowledge about Sahara-Sahel endemics and to emphasize the biological value of Mauritanian mountains as island-like mountains.

To explore the importance of gueltas as local hotspots of biodiversity, the number of vertebrates and endemics present in 69 mountain rock-pools (locally known as gueltas) were quantified and compared with species present in a surrounding area and recorded in Mauritania. Taking into account the percentage of endemics and threats, gueltas were ranked by their priority for conservation. Gueltas were considered local hotspots of biodiversity, as they are tiny places holding high number of species, including endemics, and are vulnerable to droughts and human activities. They could provide future refugia under climate change scenarios, so they are crucial for long-term conservation of Sahara-Sahel biodiversity and also for local communities, whose economy is based on water exploitation and surrounding productive habitats of gueltas.

The functional strategy of the Sahara-Sahel endemics was summarised into functional groups and their exposure to the magnitude and velocity of climate change was accessed to identify the functional groups more vulnerable by climate change. Seven functional groups with different levels of vulnerability to velocity and magnitude of climate change were identified according to their current range. Functional groups constituted by arid-adapted species combining sensitivity and low adaptive capacity, and living in flat areas, were the most threatened groups to climate change. The study provides indications on functional vulnerability to climate change in other warm deserts of the world.

Altogether, this work combined distinct methodologies applied to different biodiversity components to increase knowledge on biodiversity distribution patterns and vulnerabilities in arid environments, which ultimately can be used for designing systematic conservation programs.

KEY WORDS: arid environments; biodiversity conservation; climate change; conservation status; ecological niche models; endemics; functional groups; local hotspots; mountains; rock pools; Sahara; Sahel

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LIST OF ABBREVIATIONS

Abs	Absences
AFR	Afrotropical
AIC	Akaike information criterion
ANN	Artificial neuronal networks
ANOVA	Analysis of variance
ATEM	Annual average temperature
AUC	Area under the curve
Bal	Balance between presence and absences
BARE	Bare areas
BRT	Boosted regression trees
C10	Continental model with coarse resolution
CBD	Convention on Biological Diversity
cC10	West Africa extraction
CCR	Correct classification rates
COHE	Closed to open herbaceous vegetation
COSH	Closed to open shrubland
CR	Critically Endagered
CROP	Croplands
CRVE	Mosaic cropland (50-70%) /vegetation (20-50%)
CTA	Classification Tree Analysis (CTA)
DD	Data deficient
DIUR	diurnal
ECT	Ectotherms
EGV	Ecogeographical variable
END	Endotherms
ENFA	Ecological-Niche Factor Analysis
ENM	Ecological niche models
F1	First factorial axis
FAbs	Absence dataset informed by fieldwork
FBWV	Freshwater or brackish water vegetation
FGR	Functional Group Richness
GAM	Generalized additive models
GARP	Genetic Algorithm for Ruleset Production
GBM	Boosting Model

GCM	General Circulation Models
GIS	Geographical Information Systems
GLM	Generalized linear model
GLZ	Multiple regression model
GNI	Gross national income
GPS	Global Positioning System
GUEL	Distance to *gueltas*
HERB	Herbivorous
IGN	Institut Géographique National
INSECT	Mostly insectivorous
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for the Conservation of Nature
LC	Least Concern
LHR	Large home range
LR-NT	Lower Risk – Near Threatened
MARS	Multivariate Adaptative Regression Splines
Mau	Mauritania
Mau Endemic	Mauritania endemic taxa
MaxSS	Maximum training sensitivity plus specificity threshold
MDA	Mixture Discriminant Analysis
MF	Marginality
MTEM	Minimum temperature of coldest month
MTP	Minimum training presence threshold
NDVI	Normalized Difference Vegetation Index
NDWI_P	Normalized Difference Water Indexes to permanent water
NDWI_S	Normalized Difference Water Indexes to seasonal water
NE	Not evaluated
NNI	Nearest Neighbour Index
NOCT	nocturnal
NPMR	Nonparametric Multiplicative Regression
NT	Near threatened
OMNI	Mostly omnivorous
OVI	Oviparous
pC10	C10 projected to the regional scale at fine resolution
PCoA	Principal coordinates analysis
Perm	Permutation importance

PERM	Permanente *gueltas*
PET	Annual average potential evapo-transpiration
pR10	R10 projected to fine resolution
PWET	Annual average total precipitation of wettest month
R1	Regional models with fine resolution
R10	Regional models with coarse resolution
RAbs	Random dataset of pseudo-absences
RCP	Representative Concentration Pathways
RF	Random Forests
ROC	Receiver-operating characteristics
ROCK	Consolidated bare areas
ROI	Return-on investment
SA	Surrounding area
SAS	Sahelian acacia savannah
SCI	Science Citation Index
SD	Standard deviation
SDM	Species distribution models
SE	Standard error
SEAS	Seasonal *gueltas*
SERI	Seasonal rivers
SES	Standard effective size
SEU	Evolutionarily Significant Units
SHR	Small home range
SLOP	Slope
SPCA	Spatial Principal Components Analysis (SPCA
SPVG	Sparse (<15%) vegetation or grassland
SSC	Species Survival Commission
SSI	Simple Structure index
TMAX	Maximum temperature of warmest month
TMIN	Minimum temperature of coldest month
TS	Tolerance
TSS	True Skills Statistic
UTM	Universal Transversa de Mercator
Val	Validation
VECR	Mosaic vegetation/cropland
VIVI	Viviparous

VOL	Volant
VU	Vulnerable
WA	West Africa
WABO	Water bodies
WSS	West sudanian savannah
WWF	World Wide Fund for Nature
%cont	Percentage of contribution
%G	Percentage of taxa present in gueltas
10%TP	Tenth percentile training presence threshold

Chapter 1

General Introdution

“The desert hides its beauty.
You have to go out there.
You have to look for it, and
you will find some amazing things”

Lorraine Keith

BIODIVERSITY: WHAT IS IT, WHERE IS IT, AND WHY IS IT IMPORTANT?

Biodiversity or biological diversity means the "variability among living organisms from all sources including terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (Convention on Biological Diversity 1992). Fundamentally, it is the variety of life and processes related with it on Earth, being fundamental for ecosystem functioning. Biodiversity, including the number, abundance, and composition of genotypes, populations, species, functional types, communities, and landscape units, is affected by changes in climate resource availability and disturbance and at the same time, it strongly influences the rate, magnitude and direction of ecosystems processes, ultimately affecting human well-being and sustainable development (Diaz *et al*. 2005, 2006; Hassan *et al*. 2005; Mace *et al*. 2005; Millennium Ecosystem Assessment 2005). Biodiversity, though ecosystem services, contributes directly or indirectly to humans by supporting services through: i) structural, compositional, and functional diversity (e.g.: soil formation and photosynthesis); ii) regulatory services on the production, stability, and resilience of ecosystems (e.g.: mitigate climate change effects and regulating disease, wastes, and water quality); iii) cultural such aesthetic, spiritual, and recreational; and iv) provisioning service through direct and indirect supply of food, fresh water, fiber, shelter, and medicines (Diaz *et al*. 2005, 2006; Mace *et al*. 2005; Millennium Ecosystem Assessment 2005). In addition to the important role of biodiversity in providing ecosystem services, it also has intrinsic value, independent of any human concern.

BIODIVERSITY PATTERNS

Biodiversity is heterogeneously distributed across the world. As the multidimensionality of biodiversity place innumerous quantification challenges, a variety of surrogates or proxy measures have been widely used (e.g.: the number of distinct plant functional types or the diversity of distinct gene sequences). The most commonly used is yet species richness due to the recognized significance of species as a biological logical unit and practical and ease data accessibility (Gaston 2000; Willig *et al.* 2003). Hence most of the studies on biodiversity patterns have been relying on species richness. Nevertheless in few decades, and taking advance of new technologies, it was possible

to extensively explore and review the latitudinal diversity gradient – one of the oldest patterns in ecology and biogeography (Fig. 1.1; Brown and Lomolino 1998). Now, it is clear that the tropics harbor not only more species of plants and animals, but also more diverse genomes and clades of higher taxa (e.g.: Pianka 1966; Brown and Lomolino 1998; Gaston 2000; Willig *et al*. 2003; Mittelbach *et al*. 2007; Brown 2014). The pattern is also observed in the fossil record dating back hundreds of millions of years (e.g. Crame 2001). Moreover, it does not substantially differ between northern and southern hemispheres, nor does it differ between taxonomic groups, terrestrial, freshwater and marine environments, active and passive dispersers, or ectothermic and endothermic taxa. It occurs at all levels of evolutionary differentiation, even for intraspecific genetic and phenotypic differentiation and for lineages (Gaston 2000; Willig *et al*. 2003; Mittelbach *et al*. 2007; Hawkins *et al*. 2012; Brown 2014). Nevertheless, exceptions could be found in for example species of conifers, amphipods, crayfish, voles and penguins, which are more diverse at mid- or high latitudes than in the tropics, where some are even absent (e.g. Willig *et al*. 2003). Although not universal, the latitudinal diversity gradient is clear and definitely ubiquitous, constituting one of the fundamental and striking patterns in the natural world. There are several hypotheses and combinations of those, with different levels of explanation from random to deterministic, historical to ecological, abiotic to biotic, that have been extensively discussed and reviewed (e.g.: Pianka 1966; Stevens 1989; Rohde 1992; Gaston 2000; Willig *et al*. 2003; Brown 2014). Still, there is no universal explanation, and the most likely one would probably yield all hypotheses and processes discussed so far.

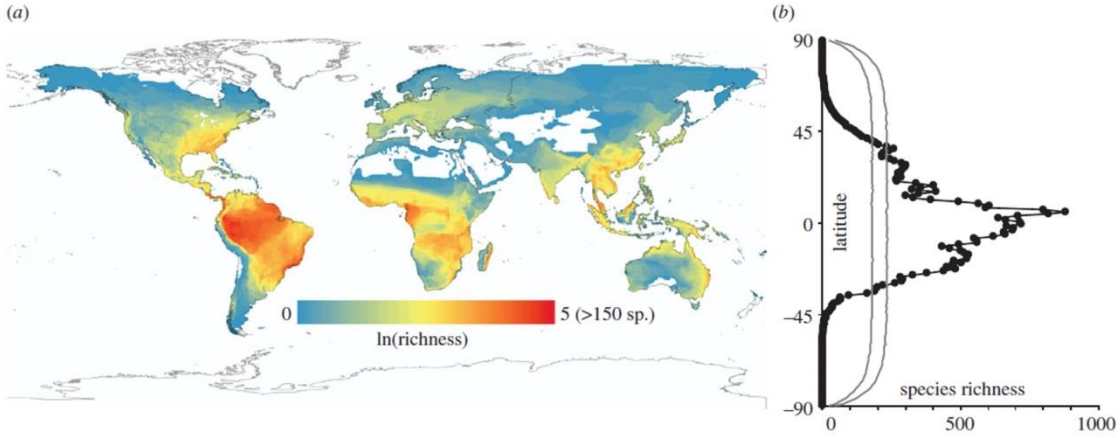

Fig.1.1 - (a) Global richness of 6117 amphibians on a log scale in 58 grid cells; (b) latitudinal distribution of species (black) compared to expectations under null models of geographical range-shuffling (grey lines showing 95% confidence intervals) (adapted from Pyron and Wiens 2013).

Biodiversity patterns follow complex patterns determined by climate, geology and the evolutionary history of the planet. At global scale, distribution patterns are mostly associated with macroclimate, while at lower scales (continental, regional or local), the distribution patterns are also related with longitude, elevation, geology, depth, and also environmental variables (topography and aridity; Gaston 2000). From global to regional scales, a host of no less important and intricate patterns of spatial variation in biodiversity disrupted the latitudinal diversity pattern. Species and ecosystems sharing similar evolutionary and biogeographic histories are geographically concentrated into *Biogeographic realms* (Fig. 1.2). Roughly corresponding to continents, they were firstly denoted in 1876 by Wallace, based on the distributions and taxonomic relationships of broadly defined vertebrate families (Wallace 1876). Although eleven realms were recently proposed based on the combination of distribution data and phylogenetic relationships (Holt *et al*. 2013), the eight terrestrial biogeographic realms based on taxa distribution are still the most commonly used classification (Fig. 1.2; Olson *et al*. 2001). Within the biogeographic realms, climatic and geological continuous areas harboring communities interacting with the physical surroundings as systems (ecosystems) are *Biomes* or "the world's major communities" (Fig. 1.2). For instance, deserts biomes may be not as species rich as tropical forests, but they yield unique assemble of species, communities and ecological phenomena (Olson and Dinerstein 2002). Nested within the biogeographic realms and biomes, *Ecoregions* correspond to large areas yielding a geographically distinct assemblage of species, natural communities, and environmental conditions (Fig. 1.2; Olson *et al*. 2001). Their boundaries encompass an area within which important ecological and evolutionary processes strongly interact (Olson *et al*. 2001; Olson and Dinerstein 2002). These large biogeographic regions intercept with each other, creating regions of rapid turnover (high beta diversity) of species and habitats – "biogeographic crossroads" (Spector 2002). Latter are areas of high species richness and beta diversity, representative of evolutionary processes such as speciation and coevolution (Spector 2002; Brooks *et al*. 2006). Biogeographic patterns, not only describe the species, communities and ecosystems arrangement across the world, but also their evolutionary history and they are ultimately representative of functional diversity patterns, as the variety of different ecological functions in a community shows patterns of association with biomes, ecosystems, and also ecoregions.

Geography's influence on local and regional diversity also produces other interesting cross-scale patterns. It has been recognized that diversity is highest not only in tropics but also in topographic diverse areas (e.g.: the slopes of the Andes and Himalayas). Topography influences speciation processes and produces fine scale variations in

climate that ultimately affect species distribution patterns (Elith and Leathwick 2009a; Wiens and Bachelet 2009; Brown 2014). Yet, at relatively fine scales, environmental variables (e.g.: productivity; evapo-transpiration) also shape the distribution of species (Gaston 2000). As it has been noticed, patterns of biodiversity distribution are complex. No single mechanism explains a given pattern, as they may vary with scale, geographical position and there is no universal pattern, without exceptions.

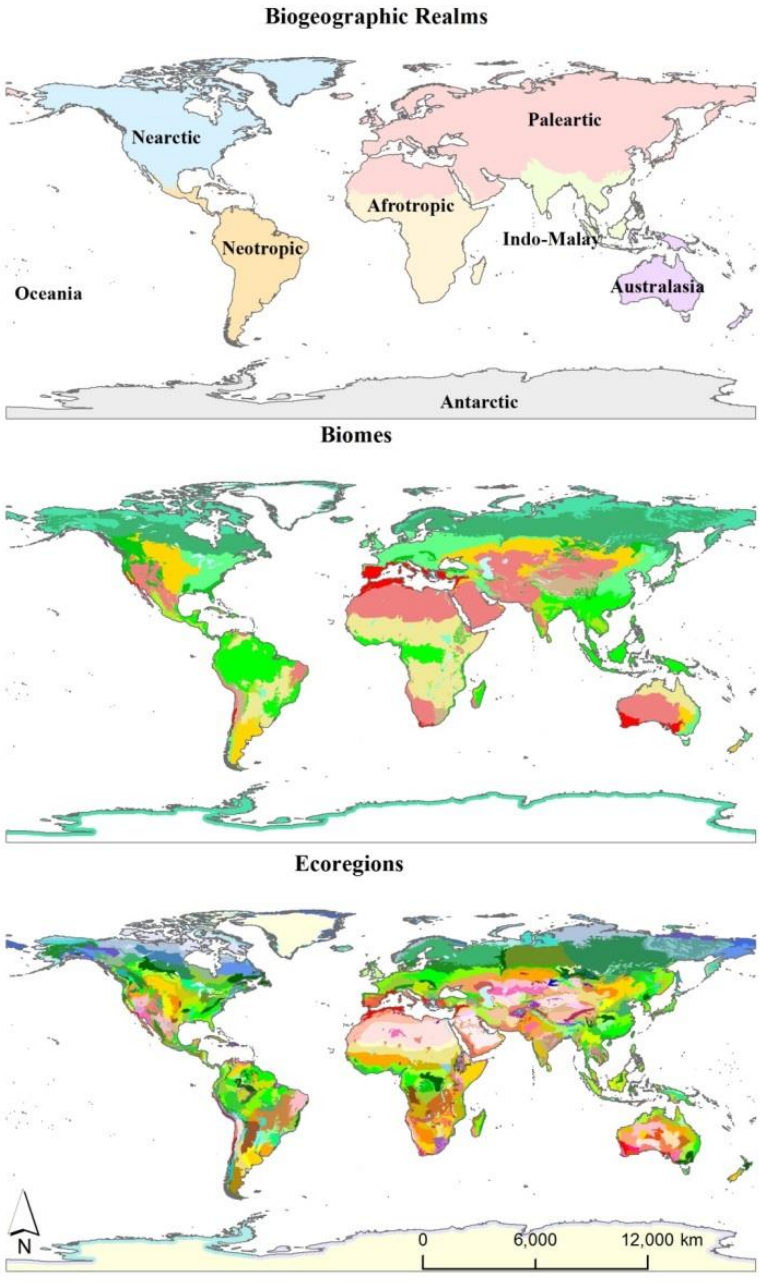

Fig. 1.2 - Biogeographic regions. From the top: eight Biogeographic realms; 14 Biomes; and the terrestrial Ecoregions (adapted from Olson *et al*. 2001).

GLOBAL BIODIVERSITY LOSS

Exceptional biodiversity loss has been reported worldwide and the current pace has been accelerating at an exceptional rate, about 1000 times the background rate of extinction or the rate of extinction in the absence of human actions (Pimm *et al*. 1995; 2006; 2014; Brooks *et al.* 2006; De Vos *et al.* 2015). From the total number of species currently described and assessed by the International Union for Conservation of Nature (IUCN 2014), 1.2% are already extinct or extinct in the wild, 0.8% are possible extinct, and 29.4% are threatened (IUCN 2014). Among vertebrates, the more threatened classes are Actinopterygii (9%), Amphibia (9%), followed by Birds (6%) and finally Mammals (5%). Magnoliopsia (38%) are the more threatened plants (IUCN 2014). Given that the absolute number of species on Earth is unknown, there are no doubts that quantified extinctions are clearly underestimated. Other dimensions of biodiversity are threatened as well. Disturbance generates changes in species, communities and resources, which have drastic consequences over functional diversity, for instance (Chillo and Ojeda 2012; MacDougall *et al.* 2013). Yet, a large proportion of world's terrestrial biomes and ecoregions are at greatest risk due to extensive habitat conversion, limited habitat protection, and habitat damaged beyond repair (Hoekstra *et al*. 2005; Millennium Ecosystem Assessment 2005).

Human actions are the major drivers of global biodiversity erosion. The human exponential growth and increased consumption are eroding the environmental services from which Earth depends (Brooks *et al*. 2002, 2008; Botkin *et al*. 2007). Several factors are synergistically contributing to the diversity depletion: agricultural expansion, urbanization, and industrial development, overexploitation, introduction of invasive species, chemical pollution; genetic depletion and humans direct elimination of top predators and other large-bodied size species, among several others (Purvis *et al*. 2000; Thomas *et al*. 2004; Millennium Ecosystem Assessment 2005; Davies *et al*. 2006; Parmesan 2006; Botkin *et al*. 2007; Ehrlich and Pringle 2008, Brooks *et al.* 2008; Bellard *et al.* 2014; Pimm *et al.* 2014). Moreover, future climatic changes are widely accepted to have the potential to exacerbate both the pace and the magnitude of biodiversity extinction, having the potential to surpass habitat destruction as the greatest global threat to biodiversity over the next several decades (Bellard *et al.* 2014). Over the last century, Earth's climate has experienced, with increasing temperatures and fluctuations in precipitation regimes, both at faster rates than anticipated (Sala *et al*. 2000; Walther *et al*. 2002; Araújo and Rahbek 2006). These climatic changes are likely to disrupt ecological processes, test species' physiological

tolerances among other consequences (Walther *et al*. 2002; Trivedi *et al*. 2008). Climatic changes are known to have affected all levels of biodiversity such genetic diversity, function diversity, species physiology, phenology, distribution and ecosystems, as well as ecosystems functionality and resilience (Thuiller *et al*. 2005; Botkin *et al.* 2007; Bellard *et al*. 2014). Despite of the variety of methods and biodiversity loss metrics available to assess climate change impacts, the majority agrees on the alarming consequences for biodiversity, with the worst-case scenarios leading to extinction rates that would qualify as the sixth mass extinction in the history of the earth (Bellard *et al*. 2014). Moreover, the continuous and accelerating biodiversity loss has consequences on ecosystem services, leading to their degradation, and the exacerbation of poverty and degradation of human well-being (Millennium Ecosystem Assessment 2005).

BIODIVERSITY CONSERVATION

Halting biodiversity erosion is priority and one of the biggest challenges posed to current human society. Aware of the urgent need to prevent biodiversity loss, 193 governmental Parties to the Convention on Biological Diversity (CBD) committed to ‘‘achieve by 2010 a significant reduction of the current rate of biodiversity loss’’. This target was missed, as the pressures to biodiversity surpassed the conservation efforts (Butchart *et al*. 2010). In response, world leaders gathered in Nagoya (in 2010) for the CBD COP10 agreed on the adoption of new and ambitious biodiversity targets and indicators for the period 2011–2020: the Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets (Secretariat of the Convention on Biological Diversity). The Strategic Plan serves as a flexible framework and comprised by five strategic goals branched in to 20 ambitious yet achievable targets, the Aichi Targets. The strategic goals are: A) address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society; B) reduce the direct pressures on biodiversity and promote sustainable use; C) improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity; D) enhance the benefits to all from biodiversity and ecosystem services and E) enhance implementation through participatory planning, knowledge management and capacity building (Secretariat of the Convention on Biological Diversity). To achieve the Strategic Goal A and B and related Aichi Targets, systematically monitoring biodiversity changes is fundamental at all scales (Pereira *et al*. 2012, 2013; Gali *et al.*

2014), as well as the identification of priority areas to where conservation efforts should be focused (Butchard *et al*. 2010; Mittermeier *et al.* 2011; Jenkins *et al*. 2013).

Theoretically and intuitively, we should conserve the more threatened areas first, while conserving resources as efficiently as possible (Murdoch *et al*. 2007; Bellard *et al.* 2014). At the global scale, the most parsimonious way is to apply the principals of irreplaceability and vulnerability to guide biodiversity conservation (Mittermeier *et al.* 2011; Bellard *et al.* 2014). The "Biodiversity hotspots" are areas that meet both principals of irreplaceability and vulnerability, as they harbor high levels of endemic species which are undergoing exceptional habitat loss (Fig. 1.3; Myers 1988, 1990, 2003; Myers *et al*. 2000; Mittermeier *et al*. 2011). Additional, they are also vulnerable to future climatic changes (Bellard *et al.* 2014), which reinforces their importance as internationally priority for conservation. Still, other large-scale conservation initiatives have attracted most of the global conservation attention, such as ecoregions (Olson *et al*. 2001), crisis ecoregions (Hoekstra *et al*. 2005), endemic bird areas (Stattersfield *et al*. 1998), centers of plant diversity (WWF, IUCN, Centres of Plant Diversity), mega-diverse countries, frontier forests (Brooks *et al.* 2006), and also the biodiversity wilderness areas (Mittermeier *et al*. 2003) and last of the wild areas (Sanderson *et al*. 2002) (Fig. 1.3). Although less threatened, the latter correspond to remote areas of high biodiversity, which have been also target of proactive conservation action because of their intactness and comparatively lower costs (Brooks *et al*. 2006; Mittermeier *et al.* 2011). Despite large scale assessments and effectiveness of global conservation, they do not identify targets for fine-scale conservation action.

In many ways, biodiversity conservation is operative at local scales. Practical conservation actions often unfold on a regional or local geographical scale, and more frequently, within political boundaries (Elith and Leathwick 2009b; Hermoso and Kennard 2012; Jenkins *et al*. 2013; Dallimer and Strange 2015). Establishment of national targets, such as sharing experiences between developed and developing countries and producing tools for successful implementation and mobilizing resources at national and sub-national levels are critical to meet the Aichi Biodiversity Targets. Despite global actions are highly valuable, an ecologically successful conservation planning should take all scales into explicit consideration (Poiani *et al*. 2000). Indeed, large scale assessments are likely to miss regional patterns and small-sized areas with large number of endemics which are simultaneously under threatened (Fensham *et al.* 2011; Murphy *et al.* 2013; Wilson and Pits 2012). At regional scales topography, induces fine scale variations in climate that influence species distribution (Elith and Leathwick 2009a; Wiens and Bachelet 2009). Ecological processes help define local species pools at regional and local scales, which are often restricted to specific micro-

habitats (Fahr and Kalko 2011). As such, regional and local conservation plans are important to identify and protected core areas, whether by their importance in terms of habitats and ecological features contained (Margules and Pressey 2000), rare or sensitive species (e.g. Wiersma 2007), focal species (e.g. umbrella species; Wiens *et al*. 2008), high biodiversity (Margules *et al*. 1988; Prendergast *et al*. 1993; Shriner *et al*. 2006), or ecological processes (Turner *et al*. 1999). Strategically targeted local conservation programs can tackle the root of extinctions (Eken *et al.* 2004), by protecting micro-habitats that are shelter to high numbers of species and endemics, which may be local hotspots of biodiversity. It is therefore critical to identify those sites where globally important biodiversity should be conserved.

The definition of priority areas for conservation is thus a major goal of global biodiversity conservation. *In-situ* conservation is recognized among the most effective means to reduce global biodiversity loss, and thus there is urgent need in identifying and ultimately ensuring that networks of globally important sites are safeguarded (Eken *et al.* 2004). Essentially, it is important to know where species live and which are the environmental features related the observed distribution patterns; which species are the most vulnerable ones and which are their threats; and which are their current levels of protection. Spatially explicit data on the ecological and geographic distribution of biodiversity (independent of its form: species, communities, functional diversity or genetic diversity) is therefore essential for global and local conservation planning and forecasting changes in current biodiversity patterns (Ferrier 2002; Funk and Richardson 2002; Rushton *et al*. 2004; Elith *et al.* 2006), and for understanding ecological and evolutionary determinants of spatial patterns of biodiversity, such as ecological corridors and past ecological and evolutionary refugia (Brown and Lomolino 1998; Margules and Pressey 2000; Ferrier 2002; Brooks *et al*. 2004; Ricklefs 2004; Graham *et al*. 2006; Jenkins *et al.* 2014). With the growing use of Geographical Information Systems (GIS), knowledge on biodiversity patterns has been steadily advanced, as better data and also methodologies become available. However, there is still a huge lack of information since much of the known species diversity has yet to be formally described and catalogued - the Linnean shortfall (Brown and Lomolino 1998), and the geographical distributions for the majority of taxa are insufficiently understood – the Wallacean shortfall (Whittaker *et al*. 2005). Plus, most of the available data is sparse and also skewed towards emblematic species, developed countries, regions of high accessibility, field stations or universities or museums (Possingham *et al*. 2000; Grand *et al*. 2007). Latter issues result in inadequate information about species distributions, which could lead to overestimated assessments and misidentification of the most priority areas for conservation.

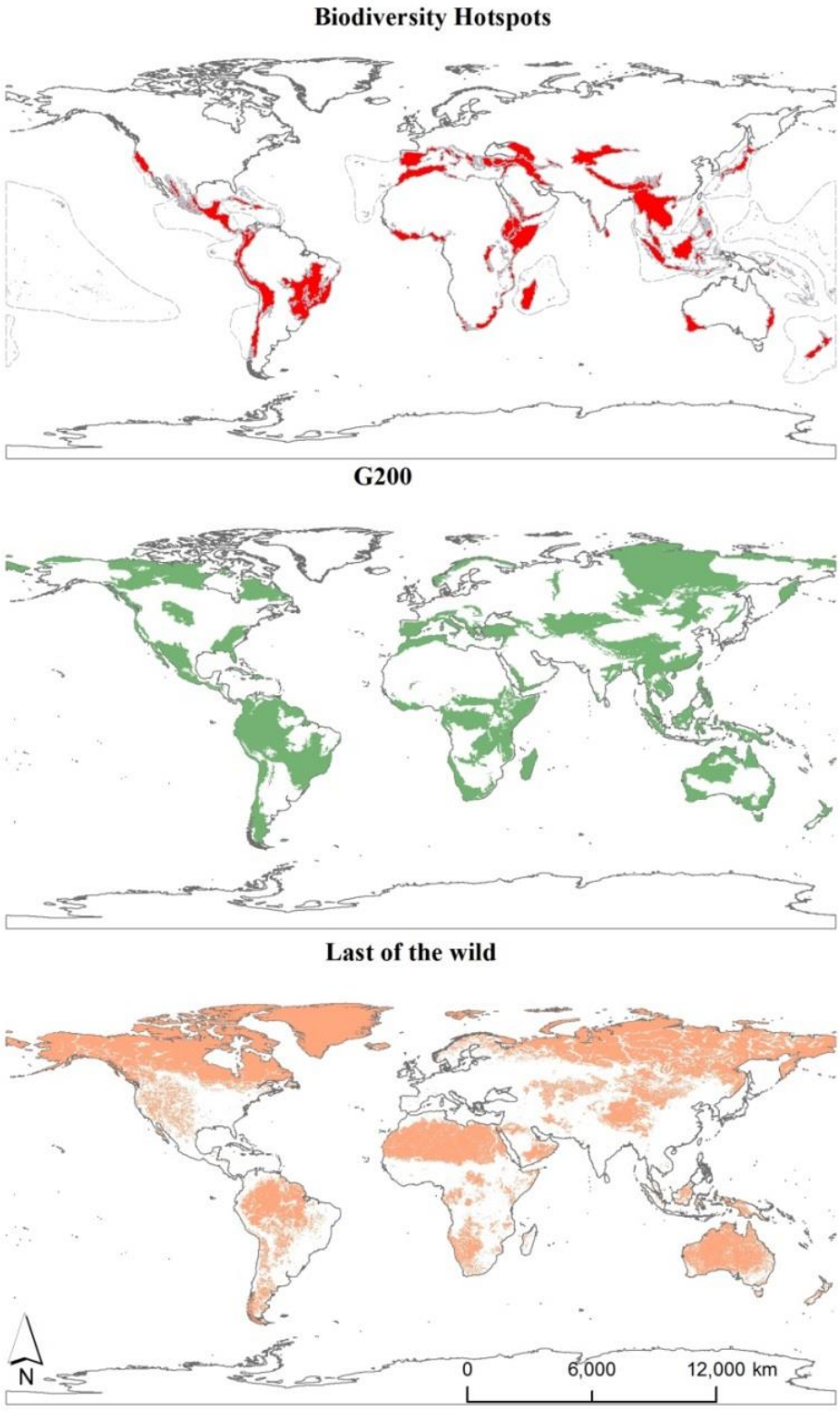

Fig. 1.3 – Distribution of three of the nine global biodiversity conservation priority templates: Biodiversity hot spots (Myers *et al*. 2000, revised by Mittermeier *et al*. 2004)]; G200, global 200 ecoregions (Olson and Dinerstein 2002); and Last of the wild (Wildlife Conservation Society 2015).

SPECIES' DISTRIBUTION MODELS TO INFORM CONSERVATION

Ecological niche models (ENMs) can greatly improve decision-making in conservation management, particularly when the ecological knowledge is incomplete. In the last decades, they have become widely applied to several fields including quantitative ecological studies (e.g.: Leathwick and Austin 2001), evolutionary biology (e.g.: Graham *et al*. 2004), population genetics (e.g.: Habel *et al*. 2015), landscape genetics (e.g.: Voda *et al*. 2015), biogeography (e.g.: Glor and Warren 2011), and climate change (Araújo *et al*. 2006; Carvalho *et al*. 2010), having the potential to play a critical role in supporting spatial conservation decision making (Margules and Pressey 2000; Addison *et al*. 2013; Guisan *et al.* 2013). The goal of ENMs is to derive model of environmental suitability for species in space and time, which is achieved by the identification of statistical relationships between species observations (presence or abundance data) and environmental descriptors (Guisan and Thuiller 2005; Elith and Leathwick 2009a; Franklin 2009; Guisan *et al.* 2013). Although the ENMs more often used are based on correlative assumptions, other mechanistic modeling approaches are also available. Latter models (e.g. based on ecophysiology or population dynamics) aim to incorporate physiologically limiting mechanisms in a species' tolerance to environmental conditions. Although they are becoming more commonly used (Kearney and Porter 2009; Kearney *et al.* 2010; Meineri *et al.* 2015), they still require more detailed data in comparison to ENMs and thus correlative approaches have been more widely used. Nevertheless, both approaches make congruent, accurate and similar predictions of current distribution of species and projections under warming scenarios (Kearney *et al*. 2010).

In the last 20 years, several methods have been developed to estimate distributional areas on the basis of correlations of known species occurrences with environmental variables. Several algorithms capable of discovering patterns are now available to this purpose, ranging from very simplistic envelope models to regression based analyses, and the more complex machine-learning techniques (Table 1.1; Guisan and Zimmermann 2000; Elith *et al*. 2006). Modeling algorithms are grouped based on the input data: whether they use only species presence data or they require both species presence and absence data. Due to uncertainties associated with absence data (Lobo *et al*. 2010; Barbet-Massin *et al.* 2012), alternative proxies of true absences have been used, including random points artificially generated in areas designated as ''non-use''' (pseudo-absences; Zaniewski *et al*. 2002; Pearce and Boyce 2005) or throughout the study area (background data; Ferrier *et al.* 2002). Envelope models require presence-

only data to build the hypervolume niche based on the locations where the species is present (Carpenter *et al*. 1993; Elith *et al*. 2006; Elith and Leathwick 2009a). The same is also true for the modified principal component analysis, a technique implemented in the Ecological-Niche Factor Analysis (ENFA; Hirzel *et al*. 2002), which rely in presence-only data for niche estimations (Table 1.1). In order to find correlations between one or more predictors and species occurrence, regression-based models have been extensively used although they require presence and absence data. As an example, linear regression tries to find linear solutions with maximum likelihood explaining the species data (Guisan and Zimmermann 2000). But the more commonly used regression-based models are the generalized linear models (GLM) by means of a link function (Guisan and Zimmermann 2000). The logit function is widely applied link function in the literature to model data that approximate a binomial distribution, as is the case of binary species presence/absence data. Generalized additive models (GAMs) are extensions of GLM models to fit non-parametric data and better describe non-linear relationships between the environmental predictors and species data (Guisan and Zimmermann 2000; Guisan *et al*. 2006; Elith and Leathwick 2009a). Machine learning methods are efficient and powerful techniques to model complex relation between species and the environment, although highly demanding in terms of computer processing. Among them are the genetic algorithms, classification and regression trees, maximum entropy, and artificial neural networks (Table 1.1). Despite the number of algorithms available, models are not free from uncertainties.

Table 1.1 Frequently used methods for identifying biodiversity distribution patterns, their main characteristics and key references. P – presence-only methods; PA – presence-absence methods. Adapted from Elith and Leathwick (2009a) and Guisan and Thuiller (2005).

Name	Algorithm	Input	Reference
BIOCLIM	Envelope model	P	Busby 1991
DOMAIN	Multivariate model	P	Carpenter *et al.* 1993
Ecological Niche Factor Analysis (ENFA)	Factor Analysis	P	Hirzel *et al.* 2002
Genetic Algorithm for Rules and Production (GARP)	Genetic algorithm	P	Stockwell *et al*. 1999
Maxent	Maximum entropy	P	Phillips *et al.* 2004, 2006; Phillips and Dudík 2008
Generalized Linear Model (GLM)	Regression	PA	McCullagh and Nelder 1989
Generalized Additive Model (GAM)	Regression	PA	Hastie and Tibshirani 1990
Multivariate Adaptive Regression Splines (MARS)	Machine learning/ Regression	PA	Friedman 1991
Nonparametric Multiplicative Regression (NPMR)	Machine learning/ Regression	PA	McCune 2006
Artificial neuronal networks (ANN)	Machine learning/ Regression	PA	Ripley 1996
Boosted regression trees (BRT) or Generalized Boosting Model (GBM)	Machine learning/ Tree/ Regression	PA	Elith *et al*. 2008; Friedman 2001; Ridgeway 2004
Random Forests (RF)	Machine learning/ Tree	PA	Breiman 2001; Prasad *et al*. 2006
Classification Tree Analysis (CTA)	Machine learning/ Tree	PA	Breiman *et al*. 1984
Mixture Discriminant Analysis (MDA)	Mixture models/ linear discriminant analysis	PA	Hastie and Tibshirani 1996; Hastie *et al*. 1995

Due to multiple sources of uncertainty, fitting ENMs requires numerous methodological and well-justified decisions. Amongst others, ENMs are sensitive to a number of scale-related issues (Guisan *et al*. 2007), such as the study area extent (restricted or complete range of species' distribution) and resolution (pixel size; Wiens 2002; Guisan *et al*. 2007). Many works have been yet discussing possible solutions to reduce both sources of uncertainty (e.g.: Thuiller *et al*. 2004; Grenouillet *et al*. 2011) and it has

been suggested that ENMs should use occurrence data from the complete species distribution range or at least from within complete biogeographical areas (Barbet-Massin *et al*. 2010). Moreover, less precise data from large representative regions provide more robust models in comparison to models built using systematically sampled data from restricted regions (Braunisch and Suchant 2010). The inclusion of the complete species' environmental range in ENMs is to be considered the best strategy to predict species-environment interactions for different regions or time periods from where the models were built (Pearson *et al*. 2002; Thuiller *et al*. 2004; Barbet-Massin *et al*. 2010).

The ecological and biogeographic context emphasizes scale-related issues affecting models accuracy. At global scale, species distributions are shaped by climate, but at regional and local scales, abiotic and/or biotic factors rather than climate itself shape the distribution of species (Elith and Leathwick 2009a; Wiens and Bachelet 2009). At these levels, ecological processes (e.g.: migration, habitat selection; species interactions) contribute to the definition of species pools, particularly at the edge of species' complete environmental range where intrinsic changes in populations promote range limit shifts (Phillips 2012). In fact, species generally tend to be more abundant at the ecological core of their distribution and become rare and specialized as the availability of optimal environmental conditions decreases and/or become more extreme, like in range edge. Here, populations may be restricted to patches of suboptimal habitats, presenting local and distinct characteristics from the entire range (Braunisch *et al*. 2008). The latter could be highlighted in biogeographic crossroads (areas where biogeographic assemblages intersect), mainly between extreme ecoregions. As different factors may control species distribution in different parts of their range, the discriminatory ability of global ENMs (built with the species' complete environmental space) may be thus limited in populations inhabiting the most distinct environments at the extremes of the range. The same is also true for ecologically plastic species ranging over different biogeographical areas, whose populations may be adapted to distinct local environmental conditions within the species-range. In both cases, local conditions represent a minor part of the species' environmental range, thus global models (species' complete environmental space) built with coarser resolutions are likely to produce biased predictions at range margins (Braunisch *et al*. 2008) and overestimate local species distributions and missing finer distributional details or local distribution gaps (Osborne and Suárez-Seoane 2002; Fjeldså and Tushabe 2005; Hernandez *et al*. 2006). Nevertheless, adjusting threshold values used to convert continuous probability maps into binary may partially solve global models bias. Nevertheless, it is uncertain how threshold selection may affect local predictions

because more restricted thresholds tend to increase sensitivity while decrease model specificity (Jiménez-Valverde and Lobo 2007). Indeed, threshold selection is often an arbitrary step as their choice depends mostly on the degree intended for minimizing both commission (false positive) and omission (false negative) errors (Liu *et al*. 2005; Jiménez-Valverde and Lobo 2007; Nenzén and Araújo 2011). As conservation actions often unfold at regional and local scales, it is of major important an exhaustive scrutiny of the effects of scale-related issues and impacts of the threshold choice in ENMs performance (Braunisch *et al*. 2008; Suárez-Seoane *et al.* 2013). These effects are likely to be amplified in transition zones to extreme environments, such as in humid to desert transitions where there is a tendency for niche truncation (the availability of suitable environmental conditions is reduced) in suitable areas' availability. Although frequently overlooked by conservation prioritization, biogeographic crossroads are areas of high species richness and beta diversity, representativeness and where evolutionary processes such as speciation and coevolution may be conserved (Spector 2002; Brooks *et al*. 2006). As such, biogeographic crossroads are areas of high conservation priority where biases in ENMs are likely to occur which may in turn result in biodiversity misrepresentation during the process of setting conservation priorities in those crossroads.

CONSERVATION STATUS

The definition of species conservation status is essential for global and regional biodiversity assessments, monitoring and conservation. The International Union for the Conservation of Nature (IUCN) Red List Categories and Criteria is the world's most widely used system for gauging the extinction risk faced by species (Lamoreux *et al.* 2003; Rodrigues *et al.* 2006; Hoffman *et al.* 2008). The IUCN Red List of Threatened Species (hereafter, IUCN Red List), produced by the Species Survival Commission (SSC) highlights species that are at the greatest risk of extinction, to ultimately guide conservation responses, primarily by identifying key and priority habitats for species, sites to be safeguarded, and actions required (Rodrigues *et al.* 2006; Hoffman *et al.* 2008). Although subject of criticisms, mostly derived from the view that its classifications are based solely on expert knowledge (Possingham *et al.* 2002), the IUCN Red List evolution on over the decades has been recognized by both governmental and non-governmental organizations to set priorities, to elaborate legislation, and to guide conservation investments (Rodrigues *et al.* 2006).

The IUCN Red List criteria evolved with the incorporation of data on species threats and on species distributions and ecological requirements. Based on a series of quantitative criteria (Lamoreux *et al.* 2003) linked to range size, population size, trend and structure, geographic range, habitat requirements, and threats and conservation actions in place or need, each species is assessed and assigned to one of the following categories: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern and Data Deficient (Fig. 1.4; IUCN 2001; Vié *et al.* 2008). The IUCN Red List Criteria are clear and comprehensive and simultaneously flexible enough to handle uncertainty (Akçakaya *et al.* 2000; Rodrigues *et al.* 2006) being developed by following extensive consultation and testing, and involving experts familiar with a very wide variety of species from across the world. They can be used to assess the conservation status of any species (apart from microorganisms) at any scale (Vié *et al.* 2008). The temporal and spatial attributes of current criteria have proven useful for determining the most urgent priority areas for biodiversity conservation (Hoffman *et al*. 2008), being used in conservation planning at global scales (e.g. Rodrigues *et al*. 2004) and down to regional (e.g. Gardenfors *et al.* 2001) and local scales (e.g. Eken *et al*. 2004).

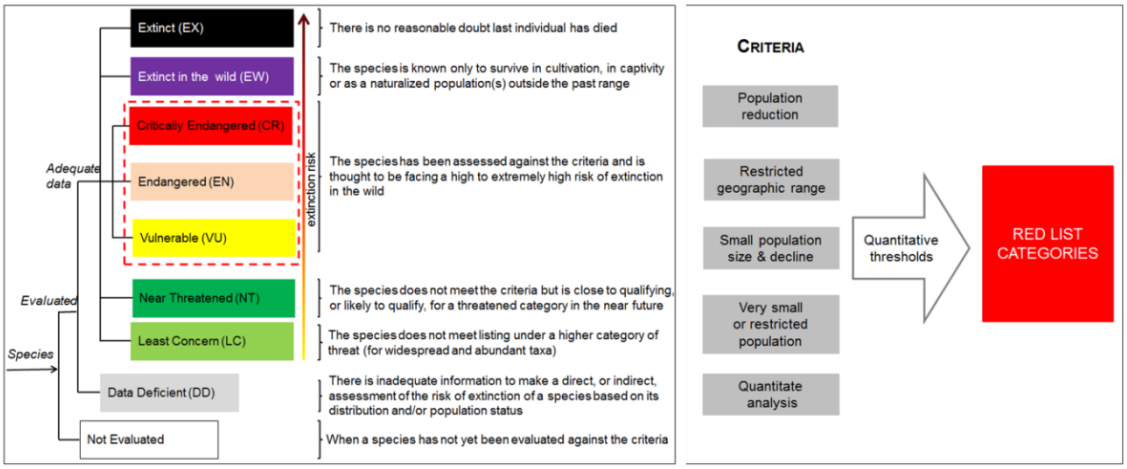

Fig. 1.4 The IUCN Red List categories and a simplified overview of the IUCN Red List criteria.

Currently, the IUCN Red List of Threatened Species is the most important mechanism for classifying species based in their extinction risk. Its framework is crucial to identify threat risks and to monitor progresses towards the Strategic Plan of the CBD (Jones *et al*. 2011; Bland *et al.* 2015). The 12th CBD's target states that by "2020 the extinction of known threatened species has been prevented" (Convention on Biological Diversity 2010). However, it is unknown the real proportion of species threatened because not all species groups have been yet evaluated and even those that were assessed,

comprise species for which little information is available, being deemed to Data Deficient (DD). According to IUCN Red List data, a species should be considered DD if the knowledge on geographic distribution, population status and trends are insufficient or lacking (IUCN Standards and Petitions Subcommittee 2014). One-sixth of the >65,000 species assessed by the IUCN are DD, which indicate that further research is necessary.

Some species have peculiar behavioral patterns or secretive habits and/or live in areas of low accessibility, being therefore difficult to detect (Hu and Liu 2014). For example, data regarding secretive and nocturnal species, such as carnivores, bats and owls tend to be more difficult to obtain in comparison to those species that are more visible and diurnal (Hu and Liu 2014).Yet, it is challenging to collect data of species inhabiting remote alpine mountains, tropical forests, polar regions or deserts. For instance, 25% of anuran species listed as DD may be found in Brazilian forests (Morais *et al.* 2013). Still, deserts are also a very good example where challenges come not only from hard environmental conditions and remoteness, but also from socio-economic and political conditions in many countries. As an example, the current paucity of knowledge about biodiversity in the African Sahara-Sahel comes from its large size, remoteness, as well as the long-term political instability which obstructs field surveys and trans-border research, together with low human development which hampers the allocation of funds to scientific studies (Brito *et al*. 2014). Nevertheless, proportions of data deficiency can significantly hinder our understanding of threat (Bohm *et al.* 2013), as taxa currently considered as DD are often rare and range-restricted, and will most likely be considered as threatened (Dudgeon *et al.* 2006; Butchart and Bird 2010). Overall, the re-assessment of DD species into different categories is very taxon-specific and depends greatly on the attitude of the assessor to risk, so that it is difficult to make any generalizations about what the future status of DD species might be. Thus it is important to gather as much information in DD species as possible, to give them the same degree of attention as to threatened taxa until their status can be assessed (Hoffman *et al*. 2008; Vié *et al.* 2008), and to understand the extent to which DD species are or not threatened to extinction. The latter might be particularly important in desert areas, where the species range is frequently restricted by strong climate controls (Ward 2009). Nevertheless, as conservation programs may neglect genuinely threatened DD species, the determination of their true conservation status is essential to developing accurate pictures of global biodiversity conservation priorities.

Accurate assessments of species and threats improve understanding of biodiversity patterns. Uncertainty associated to the level of extinction risk of DD species considerably influences understanding of global patterns of biodiversity threat and risk

(Butchart and Bird 2010; Bland *et al*. 2015). The global numbers of threatened species increased with the incorporation of the uncertainty associate to DD species (Hoffman *et al.* 2010) highlighting regions where large numbers of species with restricted distributions coincide with intensive direct and indirect anthropogenic pressures.

As conservation action and assessment are mostly global or continental, the local patterns of species richness, endemism and rarity remain less well understood (Kremen *et al.* 2008). Large-scale assessments are likely to miss regional patterns and small-sized areas with large number of endemics that could constitute local hotspots (Wilson and Pitts 2012). Yet, they often contain high numbers of DD species, which highlights the importance of regional assessments of conservation status. Given that most land-use transformation and management decisions are made at local or regional scales, overlooking these local hotspots may constitute a serious deficiency in biodiversity conservation planning.

The identification of local hotspots is particularly important in apparently homogeneous areas. Deserts and arid regions are often view as uniform areas of low diversity, being outside any global conservation initiative (Durant *et al*. 2012). However, they exhibit high numbers of species and often endemics restricted to small and fragile aquatic habitats (Davies *et al*. 2012; Murphy *et al*. 2012; Wilson and Pitts 2012). These isolated and residual water-bodies (oases, lakes and seasonal rivers) act as refugia for relict populations and constitute places where unique species evolve (Anthelme *et al*. 2008). Desertification and human activities affect water availability and threaten these water features (Jödicke *et al*. 2004; Trape 2009; Brito *et al*. 2011a). However, we know little about species richness, particularly endemics, and the threats affecting these small and isolated water features. These overlooked small size areas may in fact constitute local hotspots of biodiversity under threatened.

FUNCTIONAL TRAITS TO TRACK CLIMATE CHANGE IMPACTS

Environmental changes are persistent, causing consistent pressures on biodiversity. Human land transformation, over-exploitation, biological invasions associate to climate changes have been the main drivers of biodiversity loss in the recent past, but climate change have the potential to become the prominent, if not leading, cause of extinction over the coming century (Pacifini *et al*. 2015). Yet, the synergetic effects of all pressures are already turning more areas as exposed (Chown *et al*. 2012). Latter effects on biodiversity are broad and well document, leading to the current biodiversity extinction crises. Identify species that are likely to be most vulnerable to the impacts of

climate change is crucial to minimize global biodiversity losses (Pacifici *et al*. 2015). As novel approaches are becoming available for incorporating the combined impact human activities and climate change into policy-relevant assessments (Pereira *et al*. 2013), there are still challenges associated with species intrinsic traits and interactions with the incoming changes in the environmental conditions. Historically, the study of climate change impacts has been rooted in species concept, focusing on projections of the effects of global change on species diversity patterns (e.g.: Thuiller *et al*. 2006; Carvalho *et al*. 2010), or tracking the speed and velocity of climate contours as an expectation of how species' distributions will shift (e.g.: Loarie *et al.* 2009; Burrows *et al*. 2014). These approaches overlook the species ecophysiological responses associated with specie's sensitivity and adaptive capacity. Nevertheless, understanding the processes shaping biodiversity under multiple disturbances is still a challenge in ecology and conservation science (Mouillot *et al*. 2014). In the last years, trait-based biogeography (Functional Biogeography; Violle *et al.* 2014) has been emerging as a promising tool to simply and generically model species interactions, dispersal ability, and physiological tolerance, by tracking functional traits related to individual performance or population abundance (Chillo *et al*. 2011; Green *et al*. 2008; Mouillot *et al*. 2013; Violle and Jiang 2009; Violle *et al.* 2014). In fact, species response to climate change is mostly dependent on the level of exposure to such change (Foden *et al*. 2013), being then mediated by physiological, ecological and evolutionary traits (Dawson *et al.* 2011; Araújo *et al.* 2013; Foden *et al*. 2013). Evidences suggest life-history traits are more important than taxonomy and distribution in determining species vulnerability to climate change (Foden *et al*. 2013). On the other hand, under a changing climate, species may experience range shifts, local invasions and/or extinctions, changing communities' composition and leading to a homogenization of their functionally, and ultimately, altering local and regional ecosystem processes (Clavel *et al*. 2011, Barbet-Massin *et al*. 2015). Indeed, different consequences may arise from the gain or loss of species in a given assemblage, because the loss of few ecologically unique species is expected to have a larger ecological impact than the loss of species sharing very similar functional traits (Barbet-Massin *et al*. 2015). Under the perspective of further and rapid climatic change, an improved appreciation of its potential impact at all levels of biodiversity is urgent. As such, the incorporation of spatially and taxonomically explicit ecophysiological traits in assessments of climate change impacts would likely improve the identification of the most vulnerable species (Chown and Hoffman 2013) while locating those species would likely enhance the signalization of those which are more exposed (Foden *et al*. 2013; Pacifini *et al*. 2015). Together, they will allow a more accurate assessment of species' vulnerabilities;

having strong implications to biodiversity conservation, particularly at local scale (Chown and Hoffman 2013).

Once exposed, particular biological traits are likely to select among the most vulnerable species to environmental changes. Climate changes act as selective pressure on species whose persistence depend on the level of exposure to such changes, i.e. extent of each species' physical environment is affected; their sensitivity, i.e. the lack of potential for a species to persist in situ; and adaptive capacity, i.e. the species' inability to avoid the harmful impacts of climate change through dispersal or micro-evolutionary change (Fig. 1.5; Foden et al., 2013; Moritz and Agudo 2013; Willis et al., 2015). Under the predicted magnitude and increasing velocities of climate change (Loarie *et al*. 2009; Burrows *et al.* 2011; IPCC 2013; Garcia *et al.* 2014; Serra-Diaz *et al*. 2014), species more exposed to changes with high sensitivity and low adaptive capacities would be the most vulnerable ones (Fig. 1.5; Foden *et al.* 2013). Species range location is likely to limit the species level of exposure. As an example, species living in lowlands in desert biomes, where high velocities of climate change are expected (Loarie *et al*. 2009), are potentially more exposed. Latter might be emphasized if species exhibit low adaptive capacities (low dispersal abilities, for instance), as they will likely interfere with their ability to keep pace with moving suitable climates and thus their persistence (Walther *et al.* 2002; Massot *et al*. 2008). In fact, species dispersal ability is perhaps one of the most decisive parameter in determining species resilience to climate change. Some species might be able to follow their suitable environments without any evolution, although this is very unlikely, particularly for species occupying fragmented habitats (Chevin *et al*. 2010). Under climate change, species with fragmented ranges limited by dispersal barriers or which disperse slowly relative to the rate of environmental change are unlikely to persist (Gottfried *et al*. 1999; Massot *et al*. 2008; Chevin *et al*. 2010). Some arid-adapted ectotherms exhibit relatively sedentary behavior (Barrows 2011), which may be decreased by the environmental changes. For instance, lizards' dispersal is strongly affected by increasing temperatures (Massot *et al*. 2008). Environmental changes might also reduce species adaptive capacities, indirectly. As an example, small mammals may need to spend increased energy to control body temperature, compromising their reproduction success and dispersal capacity (Gaines and MacClenagham 1980). Nevertheless, species persistence under future climate change is also related with their sensitivity either by ecological (Root *et al*. 2005) or evolutionary processes (Bradshaw and Holzapfel 2006; Skelly *et al*. 2007). Thermal physiological tolerance, range size and local abundance are biological traits related species persistence under climate change (Walther *et al*. 2002; Calosi *et al*. 2008; Williams *et al*. 2008). Species

with restricted ranges or small population sizes are predicted more sensitive to environmental change. Latter might well be the case of some endotherms in arid environments. When environmental temperatures depart from the thermoneutral zone (range of temperature values in which the rate of metabolism of an organism is constant, McNab 2002), endotherms spend a large portion of energy to control body temperature, reducing energy available for other fundamental functions such as growth and reproduction (Boyles *et al*. 2011). Yet associated with abundance, generation time is known to constrain species' sensitivity (Chevin *et al*. 2010, Seebacher *et al*. 2014). In fact, the capacity of species to respond quickly enough to climate change is uncertain because their sensitivity imply genetic and non-genetic changes in biological traits (Burrows *et al*. 2011; Hoffman and Sgrò 2011; Duputié *et al*. 2015). Short-living species may successfully respond if the speed of climate change is slow (Lance 2009; Chevin *et al*. 2010, Seebacher *et al.* 2014). On the contrary, long-living species usually have slow genetic adaptation and may cope with the environmental changes, through phenotypic plasticity (Duputié *et al.* 2015). Despite of this, latter depends on the species geographical and climatic spaces, where species' fitness is not null (Duputié *et al.* 2015). Moreover, intrinsic ecophysiological limits may constrain species possible response to the predicted warming. Species may be more able to tolerate and adapt to changes in low temperatures regions than at higher temperatures, as hard physiological boundaries may constrain the evolution of their tolerances to high temperatures (Araújo *et al.* 2013). If upper limits are relatively narrow, the predicted increasing temperatures are likely to be responsible for widespread population changes and possible extinctions (Hoffman *et al*. 2013). For instance, in arid environments some species might have already approach their thermal physiological thermal limits (Barrows 2011) and ectotherms might be particularly vulnerable because they regulate their body temperature directly from external sources, such as solar radiation and the surrounding air (Ferri-Yáñez *et al.* 2015). Nevertheless, the risk of extinction of ectotherms might be relatively low if upper limits are not constrained, which may allow responses via evolution, plasticity and/or other mechanism responsible for increasing genetic variation (Hoffman *et al*. 2013). Species living in areas subject to past climatic fluctuations may however exhibit enhanced adaptive capacity or phenotypic plasticity to handle with climate changes, in comparison to those living in more stable environments (Tewksburye *et al.* 2008). Despite evolutionary history and physiological plasticity or acclimation increases resilience of species to climate fluctuations, the magnitude of future climate change may outstrip species adaptive capacity (Seebacher *et al.* 2014). Moreover, genetic diversity; phenotypic plasticity, evolutionary rates and life history traits (Dawson *et al*. 2011)

might be determinant for species' sensitivity and adaptive capacity under future climate change.

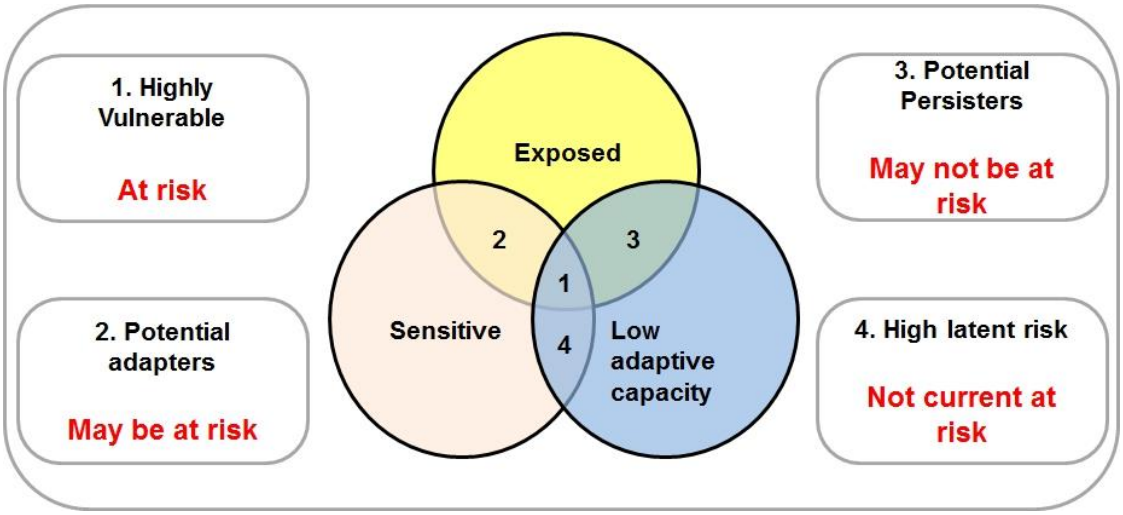

Fig. 1.5 - Framework to assess the impacts of climate change on species. Combinations of the three dimensions of vulnerability to climate change: namely sensitivity, exposure and low adaptive capacity. They describe four combinations of vulnerability to climate change: 1 - 'highly vulnerable' species, being sensitive, exposed and of low adaptive capacity, are of greatest concern. They constitute the first priority for monitoring responses to climate change and for assessment of the interventions needed to support them; 2 - 'Potential adapters' are sensitive and exposed (but high adaptive capacity) species that may be able to mitigate negative climate change impacts by dispersal or microevolution, although close monitoring is needed to verify this.. 3 - 'Potential persisters' have low adaptive capacity and are exposed (but are not sensitive) so may be able to withstand climate change in situ by themselves, but again, monitoring is needed to ensure that the assumptions about insensitivity are realized in practice; 4- species of 'high latent risk' have low adaptive capacity and are sensitive (but are not exposed) (Adapted from Foden *et al*. 2013).

Deserts are usually highly variable systems, where convergent evolution of traits and/or adaptive processes is expected, which promote functional redundancy (stability hypothesis; Rodríguez and Ojeda 2014) and provide insurance to the system (Chillo *et al.* 2011). Species adapted to extreme conditions are expected to converge in physiological traits due to the limited number of ways in which an organism can adapt to harsh conditions (Bickford *et al*. 2006). The progressive aridity conditions will likely affect negatively desert biodiversity, as it happened in the past. Past climatic oscillations in the Sahara-Sahel have greatly shaped the current distribution of biodiversity (Dumont 1982; Le Houérou 1992, 1997; Drake *et al*. 2011). Moreover, despite being arid-adapted species, they might be already in the critical thermal limit, or they might be sensitive and have low adaptive capacities, which may hamper responses to the predicted changes. It is thus important to identify groups of species gathering combinations of functional traits that may be related to vulnerability to future climatic change, in order to design regional proactive conservation plans.

THE SAHARA-SAHEL

The Sahara desert and the arid Sahel are two major arid regions of North Africa (Fig. 1.2 and 1.6a; Olson *et al*. 2001), which exhibit unique features that distinguish them from other warm deserts and arid regions worldwide. The Sahara is the largest warm desert in the world with land coverage of about 9 million km2, and together with the arid region Sahel, they cover about 11 million km2. The region is characterized by high topographic heterogeneity, from salt pans below sea level to high-altitude peaks distributed along a system of 'mountain-sky islands' (Fig. 1.6a, UNEP 2006). The climate is also heterogeneous, resulting from considerable spatial variability in temperature (Fig. 1.6; average annual temperature ranging from 9.4 to 30.8◦C) and precipitation (Fig. 1. 6, average annual total precipitation up to 981 mm; both from www.worldclim.org). Since the Pliocene (5.3 to 2.5 Mya), the region was subjected to strong climatic oscillations, shifting between dry and wet periods (Le Houérou 1997, Wang *et al*. 2008; Claussen 2009, Brito *et al*. 2014). The last humid period occurred during the mid-Holocene, when the region was covered with extensive vegetation, lakes and wetlands (Gasse 2000; Kröpelin *et al*. 2008). The last humid cycle end up with the increase of aridity, disappearance of mesic vegetation communities, and the decreased of lake levels (Foley *et al*. 2003; Holmes 2008). The establishment of the ongoing arid conditions in the Sahara was estimated around 7 million years ago (Mya) in Chad (Schuster *et al*. 2006) and around 6 to 2.5Mya in western areas (Swezey 2009). Latter climate and land-cover oscillations have greatly shifted the limit between the Sahara and the Sahel regions, having profound effects on biodiversity patterns (Dumont 1982; Le Houérou 1992, 1997; Drake *et al*. 2011). The current location of the border between the Sahara and the Sahel overlap with a biogeographic crossroad between the Palearctic and Afro-tropical biogeographic realms (Fig. 1.2 and 1.6a; Olson *et al*. 2001; Holt *et al*. 2013), and with a transition zone between two major biomes – Deserts and Xeric Shrublands and Tropical and subtropical grasslands, savannas, and shrublands (Fig. 1.2 and 1.6a; Olson *et al*. 2001). The region's biogeographic location resulted in a latitudinal variation in species distribution and increased local biodiversity (Dumont 1982; Le Houérou 1992). Despite its uniqueness, the Sahara-Sahel spread over ten countries, rated as low development (Fig. 1.7; UNDP 2010) and characterized by long-term political instability (Ewi 2010; Walther and Retaillé 2010; Lohmann 2011; Brito *et al*. 2014), which associated with its large size,

and remoteness, have contributed substantially to a generalized lack of knowledge about its biodiversity.

The Atlantic Sahara-Sahel (Western Sahara-Sahel) is characterized by a latitudinal gradient in temperature and precipitation which is disrupted by four mountain massifs (all below 900 m) with distinct climatic characteristics and vegetation affinities (Fig. 1.6b). The Adrar Atar is the northernmost mountain and represents an “island” with vegetation of Palearctic affinity, surrounded by the harsh Sahara desert (Monod 1952; Villiers 1953; Dekeyser and Villiers 1956; Barry *et al*. 1987). The southern Tagant, Assaba and Afollé mountains have a wetter climate and vegetation has Sudanese affinity (Munier 1952; Toupet 1966; Telléria *et al*. 2008). While Adrar Atar is completely isolated, from the southern mountains flows a network of seasonal rivers, running to the permanent and wide Senegal river (Fig. 1.6b). These temporary rivers could present suitable habitats for Afro-tropical species (Shine 2003; Shine and Mesev 2007; Cooper *et al*. 2006) and thus act as dispersal corridors, allowing gene flow between isolated populations in Mauritanian mountains and continuous populations in Mali and Senegal. Located in the upstream of narrow valleys at the base of these mountains, mountain rock pools (locally known as gueltas) are yet the major water habitat type (Brito *et al*. 2011a). Gueltas are generally small and water availability is mostly seasonal. In many of those, water is only available during the rainy season (July to September), when torrential waterfalls fill up the pools (Brito *et al*. 2011a). Latter makes them susceptible to different threats and vulnerable to future climate change. Despite the already recognized importance of these mountain-like islands and particularly of these water features for communities’ persistence in the Sahara-Sahel, little is known about their species richness, particularly their endemics, and specific threats affecting them.

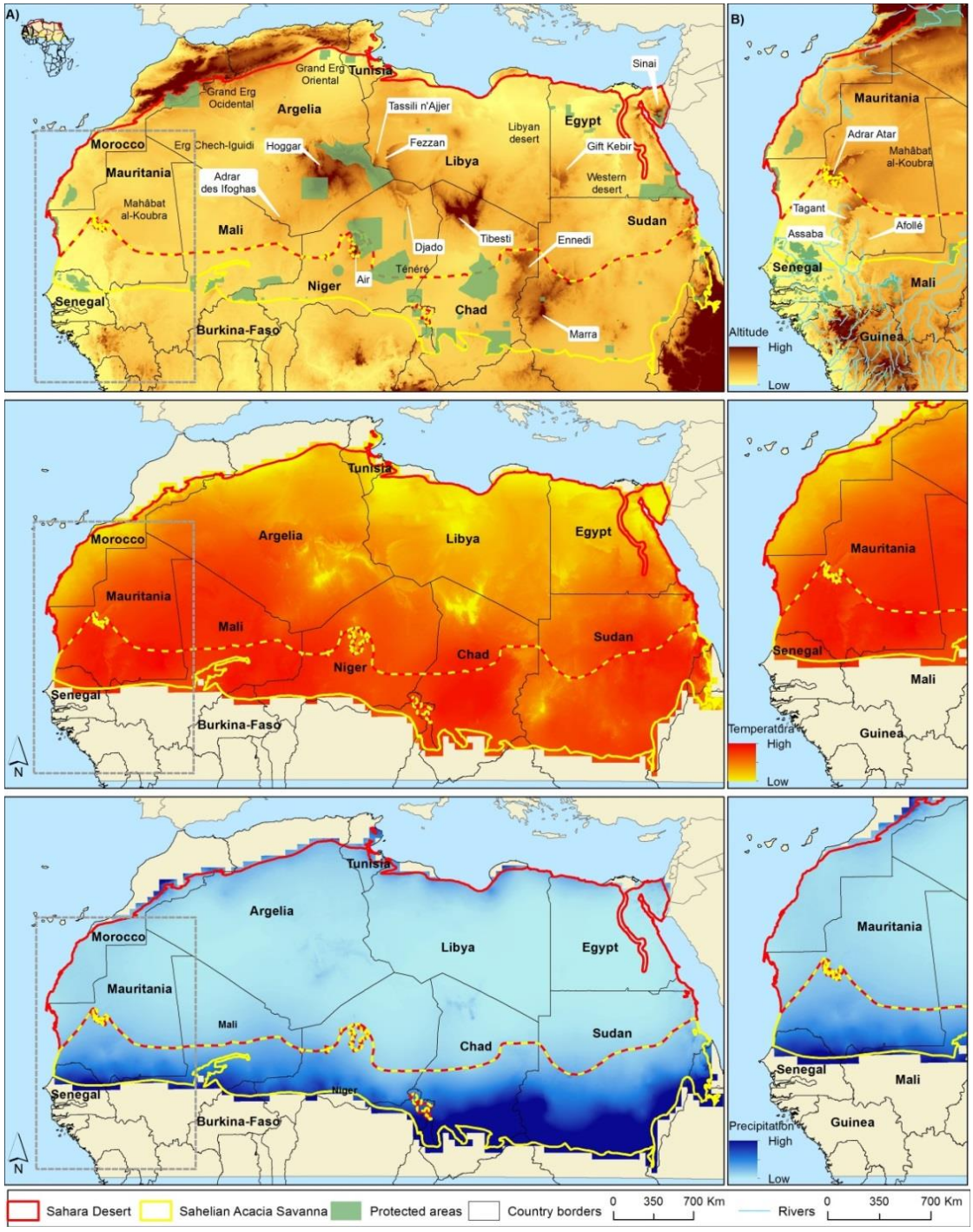

Fig. 1.6 The Sahara-Sahel study area. a) Limits of the Sahara-Sahel (Olson *et al*., 2001) and distribution of protected areas (green). Countries names are in black bold. Main mountain names (white balloons) and empty quarters of the Sahara-Sahel used in the text. b) The Atlantic Sahara-Sahel. Rivers in light blue.

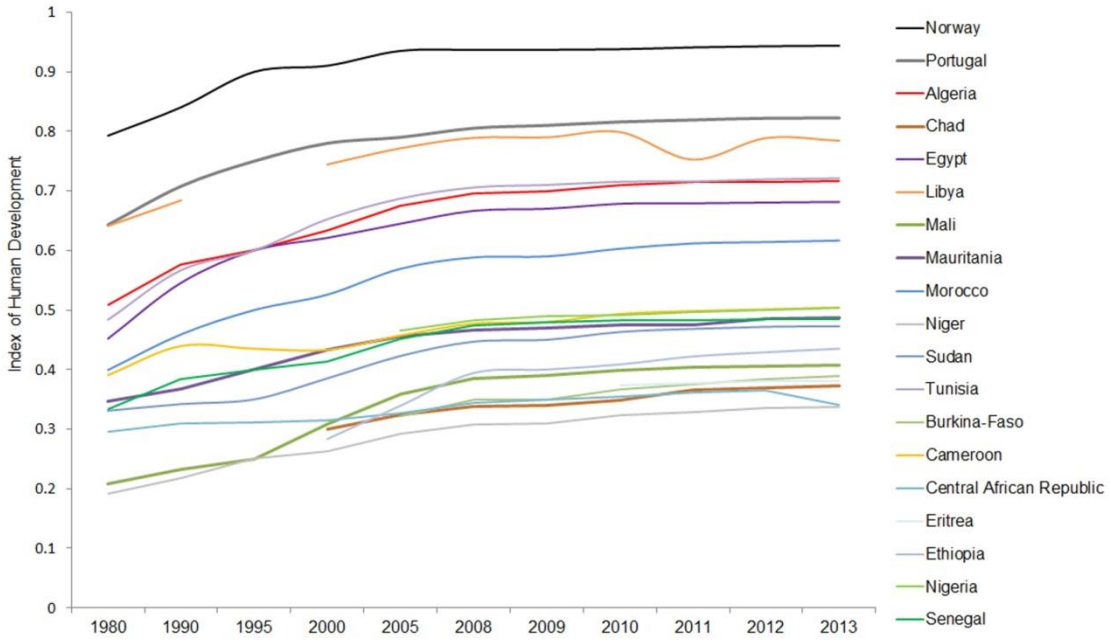

Fig. 1.7 - Index of Human Development of all countries in the Sahara-Sahel and of Norway and Portugal for comparison.

BIODIVERSITY DISTRIBUTION

There is a general lack of knowledge about the Sahara-Sahel biodiversity. The geographic location in countries of low human development (Fig. 1.6; 1.7) have been hampered the allocation of funds for scientific studies. Additional, the long-term political instability (Ewi 2010; Walther and Retaillé 2010; Lohmann 2011) has also been obstructed field surveys and trans-border research. Latter constrains resulted in a large number of species whose knowledge on geographic distribution, population status and trends are insufficient or lacking (~22% of the Sahara-Sahel endemics are not evaluated and 16% are Data Deficient according to IUCN Red List; Fig. 1.8). Moreover, there are large areas in the Sahara-Sahel under sampled, such as northern-eastern Mauritania, northern Mali, western Algeria, southern Libya, and almost all mountainously regions. Latter is particularly evident in the Adrar des Ifoghas, Tibesti, Ennedi, and Marra mountains (Fig. 1.4), where current knowledge on species richness is particularly low due to the scarce or non-existent sampling effort (Brito *et al*. 2014). Even with insufficient knowledge about species and large proportions of area under sampled, the Sahara-Sahel displays high number of patchy distributed species often associated with potential dispersal corridors and mountain refugia (Brito *et al*. 2014). Specifically, in the Atlantic Sahara-Sahel presents a complex pattern of species

distribution and local high species richness, with species of Mediterranean, Saharo-Sindian, Sahelian and Afro-tropical affinities (Dekeyser and Villiers 1956; Trapé 2009).

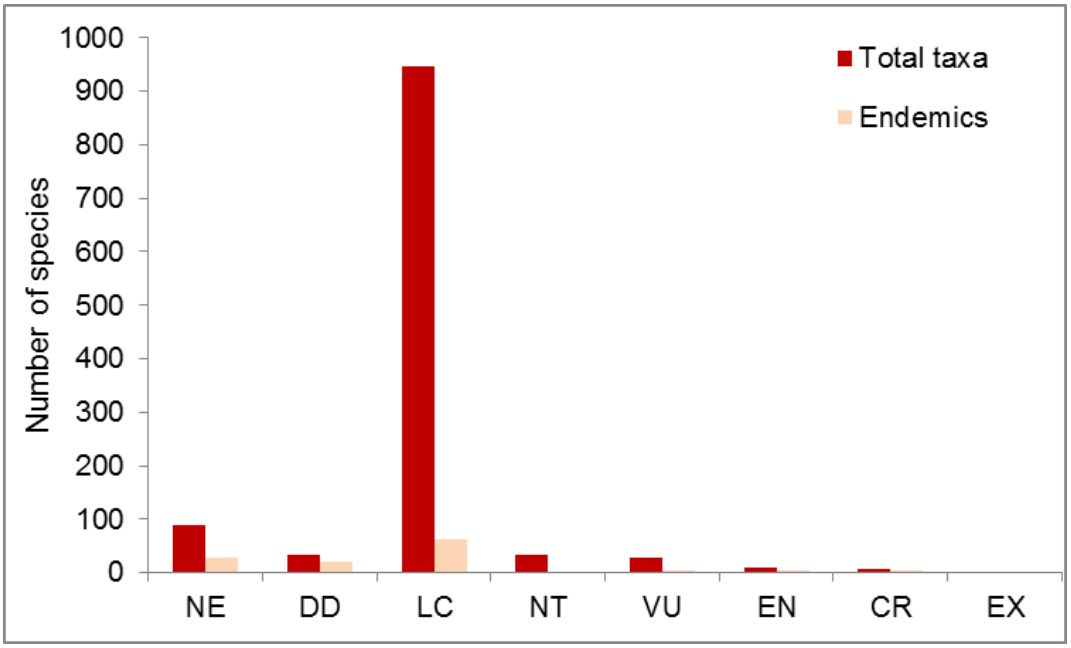

Fig. 1.8 - Percentage of the Sahara-Sahel species of each IUCN category. NE – Not Evaluated; DD – Data Deficient; LC - Least Concern; NT - Near Threatened; VU – Vulnerable; EN - Endangered; CR – Critically Endangered; EX – Extinct.

The Sahara-Sahel Mountains host more than 50% of the region's vertebrate endemics, and isolated and peripheral populations of vertebrates of non-Saharan origin (Brito *et al*. 2014). Innumerous studies in deserts and arid regions have been highlighted the role of mountains as refugia for several taxonomic groups (e.g.: Anthelme *et al*. 2008, 2011; Geniez and Arnold 2006; Tellería *et al*. 2008; Busby *et al*. 2009; Tellería 2009; Trapé2009; Brito *et al*. 2010; Brito *et al*. 2011a,b). Particularly, the central Sahara-Sahel mountains are currently refugia for threatened large ungulates and carnivores, such as *Acinonyx jubatus*, *Addax nasomaculatus, Ammotragus lervia*, *Nanger dama* and *Panthera pardus* (Busby *et al*. 2009; Wacher *et al*. 2004), probably due to their relative inaccessibility to hunters and poachers and low human activities. Moreover, the Atlantic Sahara-Sahel mountain systems allow isolated populations of Afrotropical species to persist within the Sahara-Sahel, working as biodiversity islands (Lévêque 1995; Ezcurra 2006). In fact, during the climatic oscillations mountains worked as refugia for several species from Afrotropical region whose range have expanded throughout the Sahara-Sahel during wetter periods and then remained in mountain refugia during the dry periods (Brito *et al*. 2014). Yet during the past humid cycles,

mountains were possibly connected by savannah-like habitats (Gasse 2000; Kröpelin *et al*. 2008) forming a net of biodiversity corridors (Dumont 1982; Drake *et al*. 2011). High levels of biodiversity can be found in the persisting corridors, such as the coastal Atlantic and Red Sea corridors, due to the mild climate influenced by the proximity of the sea (Brito *et al*. 2009, 2011b); or the permanent corridor, the Nile River (Brito *et al*. 2014). Additional refugia can also be found in the vast empty-quarters (unpopulated areas) and dune massifs of the Sahara, which are crucial for threatened birds, large ungulates, and carnivores that suffered extreme declines in other regions, such as *Acinonyx jubatus*, *Addax nasomaculatus* and *Chlamydotis undulate* (Saleh *et al*. 2001; Beudels *et al*. 2005, Chammem *et al*. 2012).

In the recent years, a large number of field surveys allowed increase biodiversity knowledge at several levels, by improving knowledge on species distribution or by uncovering cryptic diversity (Brito *et al*. 2014). Latter studies have been suggesting a larger number of species with much narrower ranges, frequently limited to local-hotspots of biodiversity such water bodies (Le Berre 1989, 1990; Saleh *et al*. 2001; Selmi and Boulinier 2003; Brito *et al*. 2008). In the Atlantic Sahara-Sahel, recent studies have also been calling the attention for the conservation importance of gueltas in particularly. Indeed, they hold a large number of endemic species and range-margins populations of different biogeographic origin (Trape 2009; Brito *et al*. 2011a), allowing the maintenance of rich communities, and acting as refugia to relict populations, and potential speciation drivers (Anthelme *et al*., 2008). Isolated populations of tropical and endemic species of different taxonomic groups have been reported in gueltas. These include dragonflies, such as *Ischnura saharensis* and *Trithemis annulata* (Dumont 1982; Ferreira *et al*. 2011); fishes, such as *Barbus macrops* and *Clarias anguillaris* (Trape 2009); amphibians, such as *Hoplobatrachus occipitalis* and *Amietophrynus xeros* (Tellería 2009; Padial *et al*. 2013); reptiles, such as *Crocodylus suchus*, *Ptyodactylus ragazzi*, *Python sebae* and *Varanus niloticus* (Padial and La Riva 2004; Padial 2006; Brito *et al.* 2011b); birds, such as *Burhinus senegalensis* and *Hieraaetus spilogaster* (Tellería 2009); and mammals, such as *Felovia vae*, *Procavia capensis* and *Papio papio* (Padial and Ibáñez 2005; Brito *et al*. 2010). Nevertheless, improved knowledge on the biodiversity levels in gueltas is important to assess their role as local biodiversity hotspots.

THREATS TO THE SAHARA-SAHEL BIODIVERSITY

The synergetic effect of humans' activities and climate change are eroding worldwide biodiversity, and the Sahara-Sahel is no exception. Biodiversity extinctions and/or dramatic declines have already been documented and associated with: i) increasing hunting activities since the beginning of the 20th century and the spreading of the four-wheel drive vehicles and the firearms (Newby 1980; 1990; Newby *et al*. 1987). These were the cases of *Giraffa camelopardalis, Acinonyx jubatus* and *Oryx dammah* (Ciofolo 1995; Saleh *et al*. 2001; Beudels *et al*. 2005 respectively); ii) with conflicts related to water accessibility, such as the extinction of crocodile populations; Brito *et al*. 2011a,c); iii) with fragmentation and habitat destruction resulting from overgrazing, wood collection, conversion of natural habitats into pastures and agricultural fields in large portions of the Sahel (ECOWAS and SWAC-OCDE 2006); iv) with the extraction and prospection of natural resources (oil, gas and mining; Duncan *et al*. 2014); v) land conversion due to industrial activities; and vi) associated threats from armed conflicts (Wall *et al*. 2013; Zedany and Al-Kich 2013).

Humans' activities and climate change threat gueltas independently or in synergy, having profound effects on biodiversity. Effects on gueltas and their biodiversity were already documented and associated with the droughts of the 1970s (Brooks 2004; Anyamba and Tucker 2005). In fact, some gueltas in the Adrar Atar Mountain have dried out (Trape 2009) while some water-dependent species diversity and population sizes were reduced (Jödicke *et al*. 2004; Trape 2009; Brito *et al*. 2011a). Also, the droughts of 1970's have leaded to decreasing the nomadic lifestyle in favor of sedentary habits around permanent water bodies, which have resulted in the overexploitation of gueltas and producing several conservation problems, including shortage during the dry season, fecal contamination, excessive eutrophication, and increased activities for excavating pools or pumping water (Tellería *et al*. 2008; Brito *et al*. 2011a). The combined effected of human activities and the predicted warming trend may have alarming consequences on gueltas' biodiversity.

Global warming constitutes a major threat for Sahara-Sahel biodiversity with potential to accelerate of the pace of its loss. Desert biodiversity is already under to strong climatic control while it is particularly exposed to the predicted warming, as deserts are among the most exposed biomes where the predicted amplitude and velocity of climate change will be higher (Hulme *et al*. 2001; Loarie *et al*. 2009). Recent studies with migrant passerines and breeding birds have predicted extensive range contractions and species loss across the Sahel and the northern margin of the Sahara, respectively

(Barbet-Massin *et al*. 2009; Barbet- Massin *et al*. 2010). Current protected areas are also expected to lose suitable climate for African mammals (Thuiller *et al*. 2006). A few studies developed in the Sahara-Sahel have reported negative population trends and range shifts constrained by the species' ecophysiological traits (e.g.: Wezel 2005; González *et al*. 2012, Trape 2009, Brito *et al*. 2011a, Thiam *et al*. 2008). However, quantifications of species range shifts and population trends are still scarce, and knowledge about levels of exposure to climate change based on physiological, ecological and evolutionary traits is unavailable. Although biodiversity in the Sahara-Sahel species is composed of arid-adapted species, they might be close to their critical thermal limit, or exhibiting low adaptive and dispersal capacities that may hamper responses to the predicted changes. The identification of groups of species that gather combinations of functional traits that may be related to vulnerability to future climatic change will allow designing proactive conservation plans, having strong implications to biodiversity conservation of the Sahara-Sahel.

BIODIVERSITY CONSERVATION

Biodiversity conservation in the Sahara-Sahel has mostly been neglected, even though it harbors unique species with unique adaptations to harsh and variable environments. Deserts are among the biomes less studied, being rarely viewed as conservation priority areas. Particularly, the Sahara-Sahel harbors surprisingly high levels of biological diversity, including many endemic species (some of the most endangered species in the world); relict populations, and cryptic diversity, while supplies important ecosystem services (UNEP 2006; Davies *et al*., 2012; Durant *et al*., 2012). Despite of these, it has attracted relatively little conservation finance and action (Davies *et al*., 2012), which is mirrored by lack of scientific information and knowledge on biodiversity distribution and patterns. As a direct result, many Sahara-Sahel species are not evaluated or are DD, and regional red-listing is mostly unavailable for all taxonomic groups and countries, with the exception of Morocco (Pleguezuelos *et al*. 2010). In addition, the current protected area coverage of the Sahara-Sahel (7.4%; Fig. 1.6) is below the 10% target of the Convention on Biological Diversity (Secretariat of the Convention on Biological Diversity 2010). A few studies have quantified priority areas for conservation in the Sahara-Sahel and they all agree in the need for expansion of the present conservation network (de Pous *et al*. 2011; Simaka *et al*. 2013). In the Atlantic Sahara-Sahel, protected areas are mostly located in coastal areas of Mauritania and southern regions of Mali and Senegal (Fig. 1.6; UICN/BRAO 2008). In

Mauritania, they are dedicated at preserving marine and bird fauna, and occupy around 0.2% of the country's area. Although protected areas might already provide protection for species inhabiting coastal areas, they are lacking in mountain areas. Recently, the Tagant plateau has been recognized and the "Lac Gabou et le Réseau Hydrographique du Plateau du Tagant" have been classified as a Ramsar site (Tellería 2009). Nevertheless, formal protected areas are lacking in the Atlantic Sahara-Sahel Mountains. Improved knowledge about where biodiversity concentrate and which are the environmental features related the observed distribution patterns; which species are the most vulnerable ones and which are their threats; and which are their current levels of protection are the essential roots to improve biodiversity conservation in the Sahara-Sahel.

Despite of the increasing number studies about Sahara-Sahel biodiversity and its conservation, there is still a huge lack of knowledge about biodiversity distribution patterns and status, as well as, threats, which hamper the implementation of biodiversity conservation plans. Ecological niche-based models (ENMs) using high resolution data are valuable tools and have been applied to increase knowledge about the distribution of elusive species distributed across remote areas, such as canids and vipers, for instance (Brito *et al*. 2009, 2011b). However, and due to its location in a biogeographic crossroad, the Sahara-Sahel exhibits isolated populations of non-Sahara origin living at the edge of their range, presumably in suboptimal environmental conditions. For range margin population and ecologically plastic species, whose populations may be adapted to distinct local environmental conditions within the species-range, the discriminatory ability of ENMs may be limited and affected by scale related issues. Understanding which methodologies are best to improve the performance of ENMs will provide the means to accurately identify suitable areas for range margin and isolated populations, and also for ecologically plastic species. The application of ENMs allows the identification of the environmental variables related with species distribution, suitable areas, providing important information to evaluate the conservation status of not-evaluated species or update the conservation status of those currently consider data deficient. Accurately update species conservation status improve understanding of biodiversity patterns. The identification of local hotspots of biodiversity will also increase knowledge on Sahara-Sahel biodiversity patterns and threats. Moreover, as biodiversity hotspots are conservation priority areas, their identification within the Sahara-Sahel give clues about the most priority areas for

biodiversity conservation and to prioritize the allocation of conservation founds. Finally, desert biomes are predicted to experience high magnitude and velocities of climate change. As Sahara-Sahel species are expect to be exposed to environmental changes, different combinations of ecophysiological traits are likely to determine which groups of species are most vulnerable to climate change. Gathering information on the combinations of functional traits that may be related to vulnerability to future climatic change will also allow designing more effective conservation plans for Sahara-Sahel biodiversity under climate change. As the effectiveness of current protected areas network in the Sahara-Sahel is uncertainty, this work uses different methodological approaches that are intended to increase knowledge on biodiversity distribution and conservation of the Sahara-Sahel.

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Chapter 2

Objectives and thesis structure

“Look! Look! Look deep into nature and you
will understand everything”.
Albert Einstein

GENERAL OBJECTIVES

The main objective of the work is to address biodiversity conservation in arid environments, focusing on the desert areas of the Sahara-Sahel where biodiversity is under strong climatic control and is vulnerable to climate change. The main objective can be branched into four specific but relevant goals:

1) To compare the performance of ecological niche models built at different scales to predict the distribution of ecologically plastic species and of species at range margins;

2) To evaluate the conservation status of mountain restricted species;

3) To identify local hotspots of biodiversity;

4) To identify the most vulnerable functional groups to future climate change.

SPECIFIC OBJECTIVES AND THESIS STRUCTURE

This dissertation is organized in seven chapters. **Chapter 1** consists of an introduction where the subjects touched by this thesis are contextualized within current knowledge and challenges to biodiversity conservation and the importance of arid environments in these contexts. Further details on the features and history of the Sahara-Sahel, relevant to shape current biodiversity distribution patterns, are provided. The current **Chapter 2** exposes the main objectives, details the questions addressed, and describes the organization of this dissertation.

Chapter 3 is focused in the **first objective** and addresses technical issues associated to scale-related uncertainties in ecological models when working at range margins of species distribution or with ecologically plastic species. It is constituted by two manuscripts already published in international journal indexed in the Science Citation Index (SCI-journal).

Article I. is entitled “Predicting species distribution at range margins: testing the effects of study area extent and resolution, and threshold selection in the Sahara-Sahel transition zone” and it was published in *Diversity and Distributions*. This work aimed to assess differences between global and regional models in predicting species

distributions at range margins by contrasting: estimated parameters of species' niche breadth; most important environmental factors related to species distributions; probability of species occurrence; and performance of models for identifying suitable areas for species occurrence at the regional scale.

Article II. is entitled "Applying species distribution modelling to the conservation of an ecologically plastic species (*Papio papio*) across biogeographic regions in West Africa" and it was published in *Journal for Nature Conservation*. The main objective of this work was to assess how the performance of global and regional models affects predictions of the distribution of an ecologically plastic species. The Guinea baboon was used as model system and three specific questions were addressed: 1) Does the importance of variables for the species occurrence differ across biogeographic areas? 2) Does the performance of models for identifying suitable areas for the species occurrence differ in distinct biogeographic areas? 3) Does niche overlap between suitable areas predicted by regional models? Additionally, it was identified isolated subpopulations, potential areas of conflict with human activities, and degree of formal protection of predicted suitable areas to inform local conservation planning of Guinea baboons.

Chapter 4 focused on the **objective 2**, where the conservation status of endemic fauna of Mauritanian mountains was accessed. It is constituted by two manuscripts published in SCI-journals.

Article III. is entitled "Distribution, suitable areas and conservation status of the Felou gundi (*Felovia vae* Lataste 1886)", and it was published in *Mammalia*. In this work, it were identified the environmental factors related to the occurrence of *Felovia vae* were identify and suitable areas for species occurrence were quantified, with the final goal of evaluating its conservation status.

Article IV. is entitled "Distribution, suitable areas and conservation status of the Boulenger's agama (*Agama boulengeri*, Lataste 1886)" and it as published in *Amphibia-Reptilia.* In this work, it were identified the environmental variables related with the species occurrence, quantified the number suitable areas for species occurrence, and the conservation status was assessed.

Chapter 5 is composed of one manuscript published in a SCI-journal related with the **objective 3**.

Article V. is entitled “Overlooked Mountain Rock Pools in Deserts Are Critical Local Hotspots of Biodiversity” and it was published in *PLoS ONE.* In this article, it was explored the importance of mountain rock pools (gueltas) as local biodiversity hotspots in the Sahara-Sahel, by answering how many vertebrates (total and endemics) use gueltas, what factors predict species richness, and which gueltas are of most priority for conservation.

Chapter 6 focused on **fourth objective** and it constituted by one manuscript currently accepted for publication in *Global Ecology and Conservation*.

Article VI. is entitled “Desert-adapted species are vulnerable to climate change: insights from the warmest region on Earth”. This work aimed to identify which functional groups may be identified in Sahara-Sahel endemic vertebrates, and among them which are the ones most vulnerable to climate change, both in terms of the magnitude and also velocity of climate change; where the potentially most vulnerable areas are located and to which extent the most vulnerable functional groups are represented within the current protected areas network.

Finally, **Chapter 7** provides a general discussion on the subjects addressed in the previous chapters, emphasizing the general achievements and affords question to be addressed and directions for future work.

Chapter 3

Ecological niche models performance

“Everything should be made
as simple as possible,
but not simpler.”
Albert Einstein

ARTICLE I. PREDICTING SPECIES DISTRIBUTION AT RANGE MARGINS: TESTING THE EFFECTS OF STUDY AREA EXTENT, RESOLUTION, AND THRESHOLD SELECTION IN THE SAHARA-SAHEL TRANSITION ZONE[1]

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[1] Vale CG, Tarroso P, Brito JC (2014) Predicting species distribution at range margins: testing the effects of study area extent and resolution, and threshold selection in the Sahara-Sahel transition zone. Diversity and Distributions 20: 20-33.

ABSTRACT

Aim Compare the performance of continental and regional models in predicting species distributions at range margins. Selection of study area extent, resolution and threshold affects ecological model predictions. At range margins of species distribution, local populations may be restricted to suboptimal environments distinct from the species' global range, which may be missed by continental models.

Location Africa and West Africa.

Methods We analysed differences in predicted distributions at range margins of three widespread African species that in West Africa occur in peripheral populations restricted to particular habitats. We made comparisons between models built with data from the complete and restricted range of species' distributions (Africa and West Africa, respectively), with coarse and fine resolutions (10x10km and 1x1km, respectively), and classified with three thresholds of species presence (minimum training presence, tenth percentile training presence and maximum training sensitivity plus specificity thresholds). We predicted the species' distributions and quantified environmental variable importance and profile using Maximum Entropy, and estimated niche breadth parameters with Ecological Niche Factor Analysis.

Results We found differences between model types in niche breadth estimates and in also response curves of the most important variables, suggesting that fine resolution models are more accurate at selecting marginal habitats in West Africa than in Africa. The predictions of species distributions differed with model extent, resolution and threshold analysed. Models built with the complete species environmental range and with coarse resolution tended to overestimate species distributions at the edge but accuracy increased when more restrictive thresholds were used. In West Africa, independently of the resolution, the threshold value was less important for maximising agreement between predicted probabilities and observed distribution.

Main conclusions At range margins of species distributions, regional models with precise data and conservative thresholds should be preferred over continental models with coarser resolution to identify suitable areas for peripheral populations.

Key words: Africa; Ecological Niche Factor Analysis; global models; Maximum Entropy; regional models, species distribution models.

INTRODUCTION

In recent years, ecological niche models (ENM) have become widely used in several fields including evolutionary biology, climate change, biogeography, and conservation (Guisan & Thuiller, 2005; Buisson *et al*., 2010). ENMs combine species occurrence or abundance data with environmental information to predict species distributions (Elith & Leathwick, 2009). Given that model predictions are uncertain, fitting an ENM requires numerous choices and well-justified decisions (Guisan & Thuiller, 2005; Buisson *et al*., 2010; Beale & Lennon, 2012). Some of the most important factors affecting ENMs predictions are the study area extent (restricted or complete range of species' distribution) and resolution (pixel size) (Wiens, 2002; Guisan *et al*., 2007). To reduce both sources of uncertainty, many ideas have emerged (for instance, Thuiller *et al*., 2004; Grenouillet *et al*, 2011) such as ENMs should use data at least from a complete biogeographical area (Barbet-Massin *et al*., 2010). Moreover, less precise data from large representative regions provides more robust models than systematically sampled data from restricted regions (Braunisch & Suchant, 2010). To predict species-environment interactions for regions or time periods other than those where models were built, it has been shown that it is preferable to include the complete species' environmental range (Pearson *et al*., 2002; Thuiller *et al*., 2004; Barbet-Massin *et al*., 2010).

In terrestrial systems, climate dominates distributions at the global scale, but at regional and local scales, topography produces finer-scale variations in climate that influence species distribution (Wiens & Bachelet, 2009; Elith & Leathwick, 2009). Ecological processes, such as migration, habitat selection and species interactions, and stochastic events, help define local species pools at regional and local scales, which are often restricted to specific micro-habitats (Fahr & Kalko, 2011). These processes are particularly relevant at the edge of species' complete range, which may often shift due to intrinsic changes in populations (Phillips, 2012). At range limits, the distribution of local populations may be restricted to patches of suboptimal habitats, which may present local characteristics that are distinct from the species' complete range (Braunisch *et al*., 2008). As such, ENM predictions at range margins will largely depend on the environmental features at a small scale, since different factors may control range limits at different parts of the range. When local conditions represent a minor part of the species' environmental range, global models built with coarser resolutions may produce biased predictions at range margins (Braunisch *et al*., 2008), such as overestimating local species distributions and missing finer distributional details or local distribution gaps (Osborne & Suárez-Seoane, 2002; Fjeldså & Tushabe,

2005; Hernandez *et al*., 2006). These patterns could be even more pronounced in range margins located in transition zones between climatic or habitat extremes since the discriminating ability of ENMs may be affected by differences in habitat availability or selected by species (Osborne & Suárez-Seoane, 2002). The biased predictions of global models at range margins may be partially solved by adjusting threshold values when converting continuous probability maps into binary maps. However, it is uncertain how threshold selection may affect local predictions because more restricted thresholds tend to increase sensitivity but decrease model specificity (Jiménez-Valverde & Lobo, 2007). Indeed, threshold selection is often arbitrary since there is lack of general guidelines for its choice (Liu *et al*., 2005; Nenzén & Araújo, 2011) and choice depends mostly on the degree intended for minimising both commission (false positive) and omission (false negative) errors (Liu *et al*., 2005; Jiménez-Valverde & Lobo 2007). Despite complexities associated with the choice of study area extent, resolution of variables and threshold, the accuracy of ENM predictions is important because conservation measures are often carried out at local and regional scales (Wiens & Bachelet, 2009).

Our aim is to assess differences between global and regional models in predicting species distributions at range margins by contrasting: 1) estimated parameters of species' niche breadth; 2) most important environmental factors related to species distributions; 3) probability of species occurrence; and 4) performance of models for identifying suitable areas for species occurrence at the regional scale. We will analyse differences in the predicted distribution of species when models are calibrated with complete or restricted portions of the species' environmental range, with coarse or fine resolutions, and when different thresholds for model classification are used. With this work, we expect also to contribute to the local conservation planning of threatened populations of vertebrates at the Sahara-Sahel transition zone.

METHODS

TARGET SPECIES

As model systems, we used three widespread African vertebrates (two mammals and one amphibian) that in West Africa occur in peripheral and isolated populations (Fig. 3.1; Methods A.1 in Appendix A): 1) the Patas monkey (*Erythrocebus patas* Schreber, 1774) ranges across sub-Saharan Africa, with marginal populations in a few Sahara mountains restricted to productive environments around rocky pools (locally known as *gueltas*), rivers and streams (de Jong *et al*., 2009; Brito *et al*., 2010); 2) the Bull frog (*Hoplobatrachus occipitalis* Günther, 1858) ranges from southern Sahara, through East Africa to northern Zambia, with marginal populations at Sahara mountains restricted to temporary water features such *gueltas* (Rödel *et al*., 2006; Padial *et al*., *in press*) 3) the Rock hyrax (*Procavia capensis* Pallas, 1766) is distributed throughout sub-Saharan and west Arabian Peninsula, with isolated populations in Mauritanian and Algerian mountains, where it appears to be dependent on permanent water sources (Barry *et al*., 2008; Brito *et al*., 2010).

TRAINING AREAS

We selected two areas for model training: Africa and West Africa, which matches to continental and regional scales, respectively (Fig. 3.1, 3.2). The African continent corresponds to the complete species' environmental range, since it contains the entire distribution of the target species, with exception of *Procavia capensis* that can locally be found in western Arabian Peninsula (Barry *et al*. 2008) (Fig. 3.1). West Africa corresponds to the restricted species' environmental range and we defined it between 12.5ºN and 23.5ºN, and west of 5.0ºW, covering Mauritania, southern Morocco, Senegal, Gambia, and south-western Mali (Fig. A.1 in Appendix A). This region is located in a biogeographic transition between Palaearctic and Afro-tropical regions and it is characterised by a latitudinal gradient in climate and habitat, disrupted by mountains (Methods A.1 in Supporting Information), providing suitable habitats for otherwise absent widespread African species (Le Houérou, 1997).

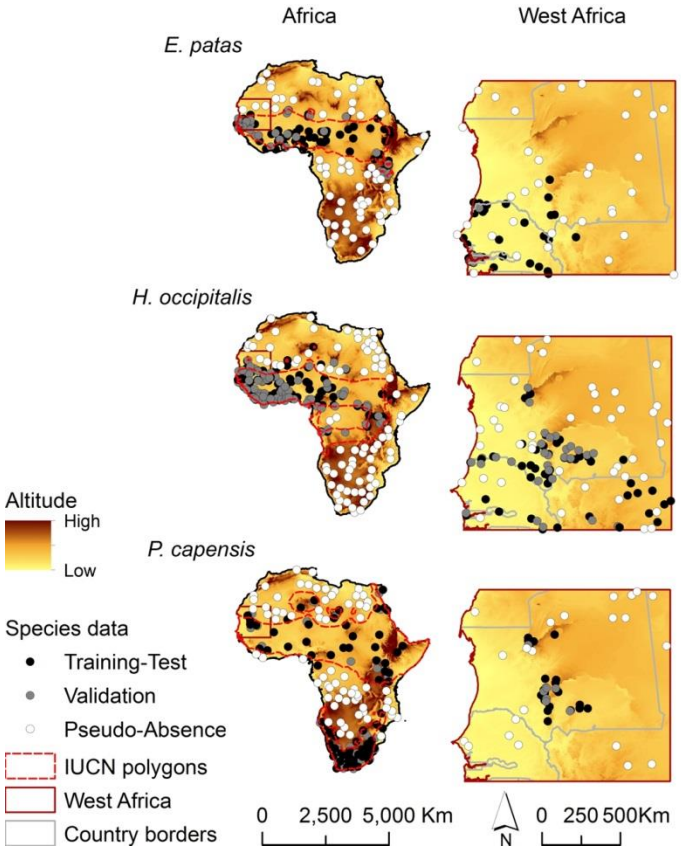

Fig. 3.1 - Distribution of training-test, validation and pseudo absences datasets of the target species in Africa and West African study areas, and location of West African study area in the African context. Location of the IUCN polygons of the target species' range.

SPECIES DATA

We used two datasets for each training area: Africa and West Africa (Fig. 3.1, 3.2), which correspond to the extensive and restricted presence datasets, respectively. For Africa, 348 species' observations (*E. patas*: N=93; *H. occipitalis*: N=150; *P. capensis*: N=105) were used for modelling purposes: 32 were collected by authors using a Global Positioning System (GPS) (Brito, 2003; Brito *et al*. 2010; authors unpub. data) and 316 constituted bibliographic observations (List A.1 in Appendix A), including georeferenced localities or clear locality names from which it was possible to assign coordinates from topographical maps (Institut Géographique National, IGN) to a precision of 10 km. Observations were randomly selected from a cluster of species occurrences and two datasets were built: 214 observations for training and testing and another with 134 observations for validating models (Table A.1 in Appendix A). In both training and validation datasets, clustering of observations was decreased by randomly removing localities that were clustered according to the Nearest Neighbour Index (NNI) given by ArcGIS 9.3 (Methods A.1 in Appendix A).

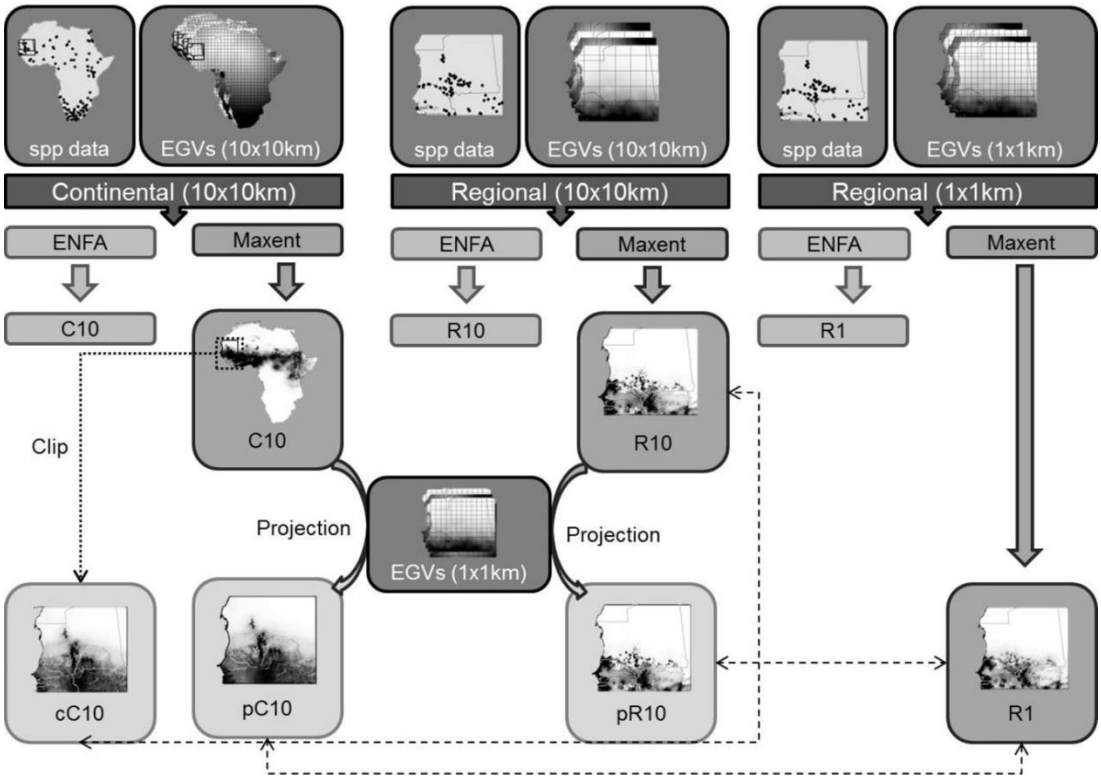

Fig. 3.2- Schematic representation of modelling strategy. Our analysis was done at a coarse resolution (10x10km) and fine resolution (1x1km) and at two different spatial extents: continental and regional. Three model types were built from species occurrences (spp data) and ecogeographical variables (EGVs), using two modelling methods (ENFA and Maxent): a continental model with coarse resolution (C10), and two regional models, one with coarse resolution (R10) and another with fine resolution (R1). We projected two Maxent models: the continental training model (C10) projected to the regional scale at fine resolution (pC10), and the coarse regional training model (R10) projected to fine resolution (pR10). We clipped the area corresponding with the regional scale from the C10 model (cC10 - represented by the squared dot line). Comparable models (same scale and resolution) are linked with dashed lines. For details see section Modelling strategy**.**

We followed the same methodology for West African data. 142 species' observations (*E. patas*: N=39; *H. occipitalis*: N=72*; P. capensis*: N=31) were used for modelling purposes: 82 were collected by authors (Brito, 2003; Brito *et al*. 2010; authors unpub. data) and remaining were gathered from bibliography (List A.1 in Appendix A). Following the same approach and according to NNI, the clustering of observations was decreased and two datasets were built: 101 observations for training models and another with 41 for validating models (Table A.1 and Methods A.1 in Appendix A).

To quantify prediction biases in ENMs, we randomly generated a pseudo-absence dataset, with the same number of observations used in the training datasets. Pseudo-absences (hereafter absences) likely corresponded with true absences because they were selected from areas outside buffers encompassing the IUCN polygons of species distribution (IUCN, 2011) and the presence dataset of each species (see details in Methods A.1 in Appendix A).

ECOGEOGRAPHICAL VARIABLES

We used the same set of 10 ecogeographical variables (EGV) in both training areas. EGVs included one topographical grid (USGS, 2006) that was used to derive Slope, with "Slope" function of ArcGIS; three climate grids (Hijmans *et al*., 2005); five distance to habitats grids derived from a land-cover grid for years 2004-2006 (Bicheron *et al*., 2008); and distance to *gueltas* digitised from the IGN maps (Table 3.1). To convert the original categorical habitat EGVs (including *gueltas*) into continuous variables, we created one binary grid for each habitat type. We calculated the Euclidean distance of each grid cell to the closest habitat type cell. All EGVs had an original square pixel size of 30" (1x1km). To create the set of coarse EGVs for African and West Africa areas, we resampled the original EGVs to ~5' (10x10km). EGVs had correlation coefficients below 0.81 in all areas and scales (Table A.2 in Appendix A).

Table 3.1 - Range (minimum and maximum) and units of environmental factors used for modelling the distribution of the target species in Africa at 10x10km (C10), in West Africa at 10x10km (R10), and in West Africa at 1x1km (R1).

Code	Description	Units	C10	R10	R1
PWET	Annual average total precipitation of wettest month	mm	0 – 1153	4 - 449	4 - 455
TMAX	Maximum temperature of warmest month	ºC	1.6 - 48.9	27.3 - 47.9	27.1 - 48.0
TMIN	Minimum temperature of coldest month	ºC	-13.6 - 23.2	8.6 - 18.8	8.5 - 18.9
SLOP	Slope	%	0 – 60	0 - 21	0 - 28
	Distance to:				
CRVE	Mosaic cropland (50-70%) / vegetation (20-50%)	º	0 - 37.1	0 - 6.5	0 - 6.6
SPVG	Sparse (<15%) vegetation or grassland	º	0 - 7.5	0 - 3.9	0 - 3.9
BARE	Bare areas	º	0 - 9.7	0 - 1.3	0 - 1.3
ROCK	Desert rocky areas	º	0 - 13.2	0 - 3.6	0 - 3.7
SERI	Seasonal rivers	º	0 - 12.8	0 - 5.5	0 - 5.5
GUEL	Gueltas	º	0 - 51.3	0 - 7.5	0 - 7.6

MODELLING STRATEGY

Our analysis was done at a coarse resolution (10x10km) and fine resolution (1x1km) and at two different spatial scales: continental that covers Africa, and regional that extends over West Africa. With this we designed three model types (Fig. 3.2): a continental model with coarse resolution (C10), and two regional models, one with coarse resolution (R10) and another with fine resolution (R1). We also projected two models: C10 projected to the regional scale at fine resolution (pC10), and R10 projected to fine resolution (pR10) (Fig. 3.2).

To quantify parameters related to niche breadth of each species in the continental and regional training areas, we performed an Ecological-Niche Factor Analysis (hereafter ENFA), using Biomapper 4.0 software (Hirzel *et al*., 2004) (for details, see Methods A.2 in Appendix A). We extracted niche breadth parameters, marginality (MF) and tolerance (TS), from each ENFA output (Hirzel *et al*., 2002).

To identify EGVs related to species' distribution in both training areas, we used ENFA and the Maximum Entropy approach, implemented in Maxent 3.0.4 beta software (Phillips *et al*., 2006). We derived models of species probability of occurrence in both training areas, using Maxent (Phillips *et al*., 2006). This technique requires only presence data as input and consistently performed well in comparison to other methods (Elith *et al*., 2006; Hernandez *et al*., 2006). We developed three models for each species using distinct training areas and pixel sizes: C10, R10, and R1. 10 model replicates were built for each model type with 10% of test data chosen by bootstrap with random seed, auto-features and logistic output (Phillips *et al*., 2006). We took the average area under the curve (AUC) of the receiver-operating characteristic (ROC) plot as a measure of model fitness (Fielding and Bell 1997). The 10 replicates were averaged to generate a forecast of species presence probability, which is a robust procedure to derive consensus predictions of species likelihood of presence (Marmion *et al*. 2009).

We determined the EGVs' importance for explaining species' distribution from their average percentage of contribution and permutation importance to each training model, and their average gain with training and test data using a Jackknife analysis. We determined the relationship between species' occurrence and EGVs by visual examination of response curves profiles from univariate models. Finally, we projected the coarse scale regional and continental models to the fine scale at the regional extent.

EVALUATION OF MODEL PERFORMANCE

To compare probabilities of occurrence for each species in continental and regional training areas, we used R software v. 2.13 (R Development Core Team, 2011) to calculate Pearson's correlations between probability models. First, we extracted the area corresponding to the regional scale from C10 model (hereafter cC10). Then, we performed comparisons between models with the same resolution: between cC10 and R10, and between projections (pC10 and pR10) and R1.

To evaluate model performance for identifying suitable areas for species occurrence, we reclassified the three training models (C10; R10 and R1), the two projections (pC10

and pR10), and the West Africa extraction (cC10) to display areas of probable presence or absence for each species, using three different threshold values for species presence. Given that threshold choices should be adjusted to the prevalence of the training data (Lobo *et al*. 2008), we selected the minimum training presence threshold (MTP) and the tenth percentile training presence threshold (10%TP) which rely only on presence data, and the maximum training sensitivity plus specificity threshold (MaxSS) which accounts both presence and absences data (Methods A.2 in Appendix A).Thresholds were then used to classify average continuous probabilities into binary maps for all areas and projections.

To calculate correct classification rates of data (CCR), we intersected both validation and absences datasets with each training model and projection, and with the West Africa extraction. CCRs were calculated for the validation and absence datasets, and balance between them, which combined both CCRs and it is given by: [(N validation + N absences)/(Nt validation + Nt absences)]*100; where N is the number of validation data or absences correctly classified and Nt is the total number of validation data or absences. Additional, we calculated the sensitivity, specificity, Kappa statistic and True Skills Statistic (TSS) for each training model and projection, and the West Africa extraction. All measures were calculated by applying the respective formulas to a 2×2 confusion matrix (for details about formulas see: Allouche *et al*. 2006). Sensitivity is the probability that models will correctly classify a presence, while specificity is the probability that models will correctly classify an absence. For the confusion matrix, TSS = sensitivity + specificity -1 (for details see: Allouche *et al*. 2006).

RESULTS

The ROC plots exhibited high average AUCs for both training and test datasets and for all model types. The average AUCs for training datasets ranged from 0.89 to 1.00 between different species, whereas for the test dataset, it ranged from 0.79 to 0.99 (Table A.1 in Appendix A).

NICHE BREADTH PARAMETERS

Overall, niche breadth estimates indicated a tendency for all species to select marginal habitats (MF>0.730) and to live in narrow ranges of environmental conditions (TS<0.686) in all model types (Fig.3.3). Differences were found between continental and regional models: all species tended to select more marginal habitats in R10 and

R1 than in C10 (Fig. 3.3).Tolerance scores (TS) indicated a trend for *P. capensis*, for instance, to occur in narrower ranges of conditions in R1 and R10 than in C10 (TS=0.075, 0.069 and 0.686, respectively) (Fig. 3.3).

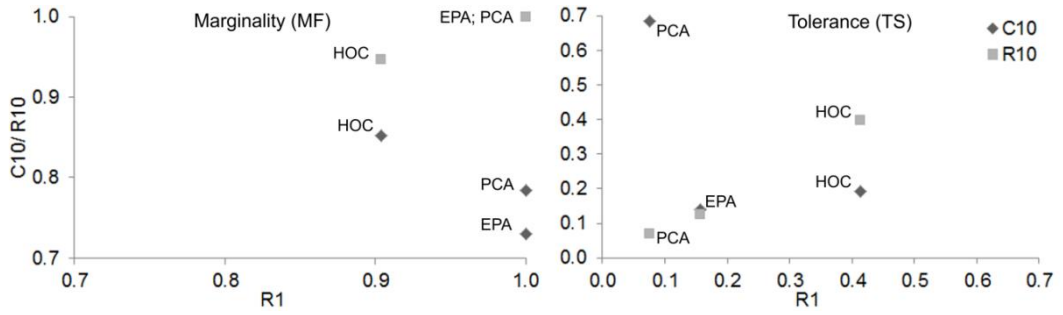

Fig. 3.3- Marginality and tolerance scores derived from ecological-niche factor analysis for the target species according to three model types: continental and regional at coarse resolution 10x10km (C10 and R10, respectively), regional at 10x10km (R10), and regional at fine resolution1x1km (R1). EPA: *Erythrocebus patas*; HOC: *Hoplobatrachus occipitalis*; PCA: *Procavia capensis*. MF: Marginality score; TS: Tolerance score.

IMPORTANCE OF ENVIRONMENTAL FACTORS

The percentage contribution, the permutation importance and the Jackknife evaluation of the three Maxent models types (C10, R10 and R1) agreed that the most important EGVs related to the distribution of each species were identical for all model types. The range of *E. patas* was mostly related to distance to mosaic cropland/vegetation (CRVE), *P. capensis* to distance to *gueltas* (GUEL) and *H. occipitalis* to both variables (Table 3.2, Fig. A.2 in Appendix A). However, particular differences were found in variable contribution between model types: for instance, the relative importance of CRVE for *E. patas* and of GUEL for *P. capensis* were higher in R10 and R1 than in C10 models, whereas the importance of precipitation of wettest month (PWET) for *E. patas* was higher in C10 than in R10 and R1 models.

The EGVs that contributed most to species marginality were also the ones with larger contribution to the Maxent models (Table 3.2). Differences were found in EGV scoring between ENFA model types: F1 scores of CRVE for *H. occipitalis* and of SLOP for *P. capensis* were higher in R1 than in C10 models, whereas scores of PWET for *H. occipitalis* and CRVE for *P. capensis* were higher in C10 than in R1 models.

Response curves of variables that contributed the most exhibited different patterns across model types for each species: presence probability tends to change more abruptly in regional than in continental models (Fig. 3.4). For instance, presence probability of species decreases sharply with increasing distances to GUEL and CRVE

in R10 and R1 and more gradually in C10 models, whereas it increases abruptly with increasing values of SLOP and PWET in R10 and R1 and more gradually in C10.

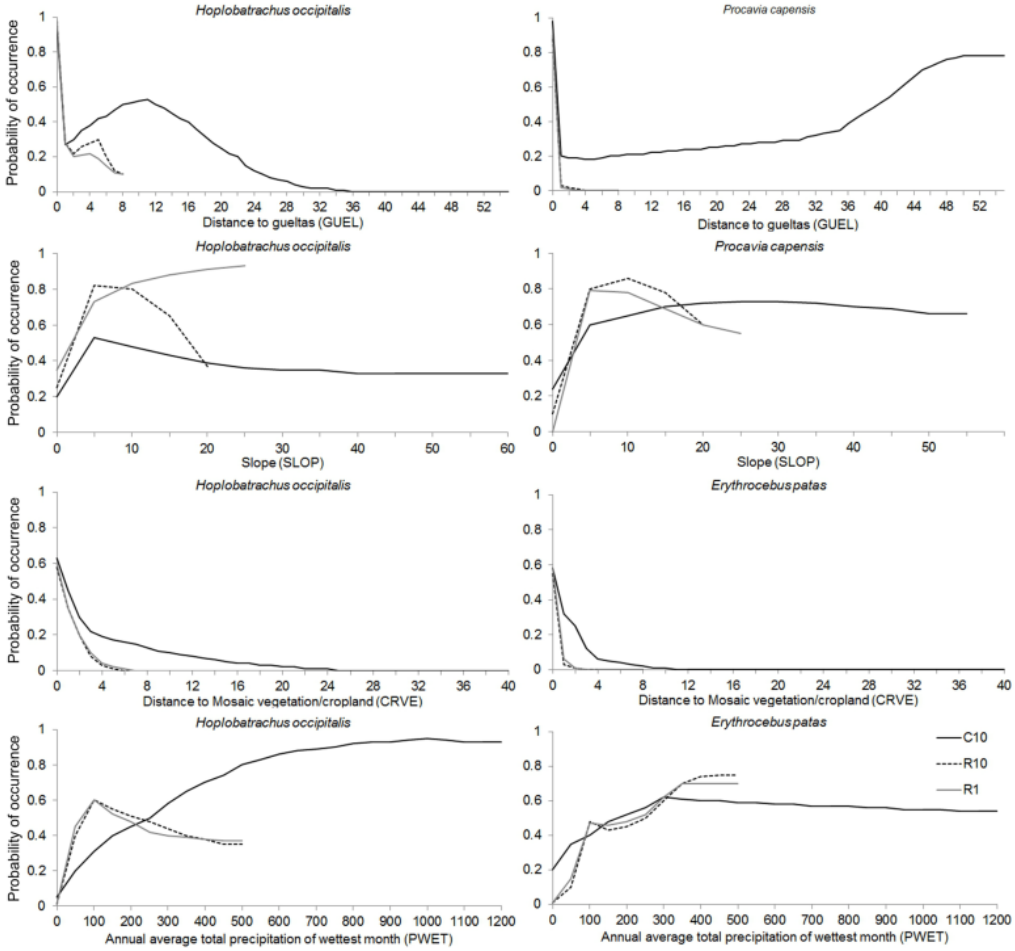

Fig. 3.4- Response curves for the environmental factors most related to the distribution of the target species in each Maxent model type: continental and regional model at coarse resolution (C10 and R10, respectively), and regional model at fine resolution (R1).

Table 3.2 - Measures of contribution of environmental variables to the ecological models for the target species. Percentage of contribution (%cont) and permutation importance (Perm) derived from maximum entropy models, and the score on the first factorial axis (F1), representing marginality, derived from ecological-niche factor analysis, is given. Models derived were the continental and regional at coarse resolution 10x10km (C10and R10, respectively), and regional at fine resolution 1x1km (R1). Explanation of variable codes is given in Table 3.1.

	Models	PWET	TMAX	TMIN	SLOP	CRVE	SPVG	BARE	ROCK	SERI	GUEL
	Erythrocebus patas										
	C10	24.7	1.0	3.4	1.0	41.6	5.0	0.6	3.6	4.0	15.0
%Cont	R10	3.9	14.8	4.7	0.7	57.3	1.6	6.9	1.6	1.9	6.6
	R1	2.7	11.3	5.6	2.6	49.7	2.5	7.6	1.3	1.4	15.4
	C10	30.7	4.3	5.4	1.1	14.1	7.0	1.0	6.1	5.7	24.6
Perm	R10	8.8	4.0	3.3	0.2	72.8	0.6	2.1	1.3	3.8	3.2
	R1	1.0	4.1	5.7	0.7	74.5	1.2	6.4	0.4	2.3	3.5
	C10	0.5	0.1	0.5	0.1	-0.4	-0.1	-0.3	0.1	-0.3	-0.4
F1	R10	0.5	-0.4	0.4	0.1	-0.4	-0.2	-0.1	0.3	-0.3	0.1
	R1	0.5	-0.4	0.4	0.1	-0.4	-0.2	-0.1	0.3	-0.3	0.1
	Hoplobatrachus occipitalis										
	C10	17.4	0.7	13.5	2.5	24.0	4.0	3.7	4.5	4.4	25.4
%Cont	R10	6.5	0.3	1.9	1.0	22.4	23.9	6.1	3.1	2.4	32.5
	R1	6.1	0.1	2.7	1.8	19.0	14.6	5.8	2.5	3.5	44.1
	C10	7.3	2.2	22.2	1.7	5.0	2.5	4.5	5.2	8.3	41.2
Perm	R10	5.2	1.3	5.0	0.4	37.2	10.7	9.1	8.2	5.8	17.1
	R1	13.0	1.5	3.8	0.8	20.7	13.1	7.1	8.3	6.1	25.5
	C10	0.6	0.1	0.5	0.0	-0.4	0.3	-0.1	0.3	-0.1	-0.4
F1	R10	0.3	-0.1	0.3	0.5	-0.4	-0.4	-0.2	0.0	-0.3	-0.3
	R1	0.3	-0.1	0.3	0.4	-0.5	-0.4	-0.2	0.0	-0.4	-0.3
	Procavia capensis										
	C10	2.8	4.1	2.1	1.9	9.4	9.1	5.0	2.9	2.7	60.1
%Cont	R10	0.6	0.4	1.8	1.0	1.1	1.7	1.3	1.8	1.3	88.9
	R1	0.0	0.1	1.7	4.8	2.2	3.2	1.3	0.9	0.8	84.9
	C10	7.0	8.0	4.6	1.3	10.4	7.2	23.8	7.4	3.2	27.0
Perm	R10	2.7	2.7	1.2	0.1	0.4	2.7	5.2	29.8	0.2	55.0
	R1	0.0	0.8	1.7	0.2	0.1	0.8	19.2	10.3	0.3	66.7
	C10	-0.1	-0.4	-0.3	0.3	0.6	-0.2	-0.2	-0.2	-0.1	0.5
F1	R10	-0.1	0.0	0.0	0.7	-0.1	-0.3	-0.2	-0.2	-0.2	-0.5
	R1	-0.1	0.0	0.0	0.8	-0.1	-0.2	-0.2	-0.2	-0.2	-0.4

CONTINUOUS PROBABILITY MODELS

Overall, the continuous probability of occurrence associated to each pixel was different between model types with identical pixel size (Fig. 3.5). The probability values for the same area in cC10 were higher in comparison to R10 predictions. The same pattern was observed between pC10 and R1 models. In other words, pixels with predicted low probabilities of occurrence in regional models were predicted by continental models with a wide range of probabilities. On the contrary, for *H. occipitalis* probability values in pR10 tended to be in agreement with R1 predictions.

EVALUATION OF TRAINING MODELS AND PROJECTIONS

The range and configuration of predicted suitable areas for each species differed between model types and applied thresholds (Fig. 3.6). Overall, C10 areas adjusted to presence data of each species. The correct classification rates (CCR) of both validation and absence datasets and the other measures (sensitivity, specificity, and Kappa and TSS statics) were high for *E. patas* and *H. occipitalis* when using the minimum training presences threshold (MTP) (Table 3.3 and Table A.3 in Appendix A). Other thresholds tended to underestimate suitable areas of these species in the C10 model, which was expressed by a lower CCR of validation data in relation to absences and by sensitivity and specificity values. For C10 models of *P. capensis*, all thresholds produced low CCRs, Kappa and TSS statistics but the maximum training sensitivity plus specificity (MaxSS) provided more balanced CCRs. The intersection of validation and absence datasets from West Africa with the cC10 model showed that suitable areas were overestimated, independently of the threshold used, expressed by low CCR of absences (Table 3.3).

Models calibrated in West Africa (R10 and R1) fitted to the occurrence data of all target species (Fig. 3.6). The CCR of validation and absence datasets, the balance between them and the other measures used were high in R10 and R1 for all species, irrespectively of the threshold used (Table 3.3 and Table A.3 in Appendix A). However for *E. patas* and *H. occipitalis*, there was a trend for overestimating suitable areas in West Africa when using the MTP threshold. Predicted suitable areas for each species were different between pC10 and pR10. Independently of the threshold selected, suitable areas predicted by pC10 were overestimated, as observed by very low CCR of absences and low specificity, with the single exception of MaxSS threshold in the case of *P. capensis*. On the contrary, pR10 predictions fitted to occurrence data of all

species and 10%TP provided the highest CCRs for the validation and absence datasets and the balance between them (Table 3.3).

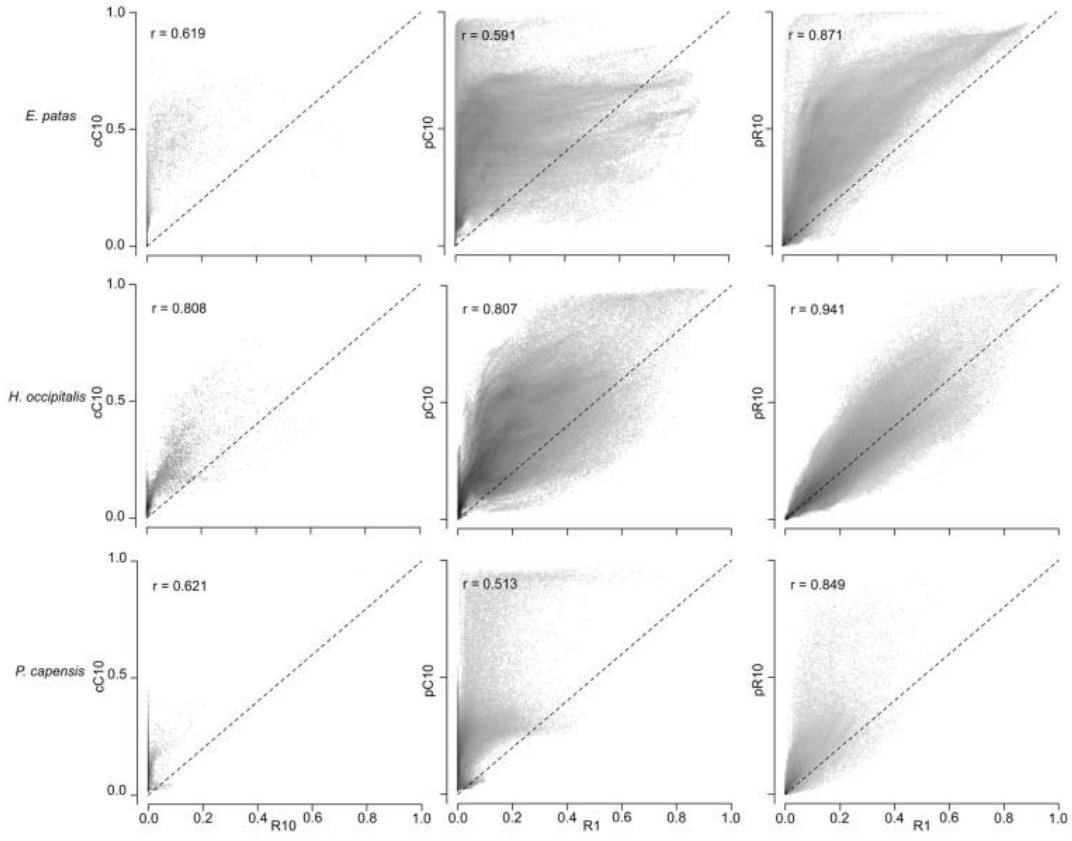

Fig. 3.5- Pearson's correlations between continuous maximum entropy probability models and projections with identical pixel size for the target species. Models represented here are the regional at coarse and fine resolution (R10 and R1, respectively, on the horizontal axis) vs. the extraction of coarse resolution continental model and projections of coarse resolution regional and continental models (C10 Clip, pR10, pC10, respectively, vertical axis). The y=x line is shown (dashed line).

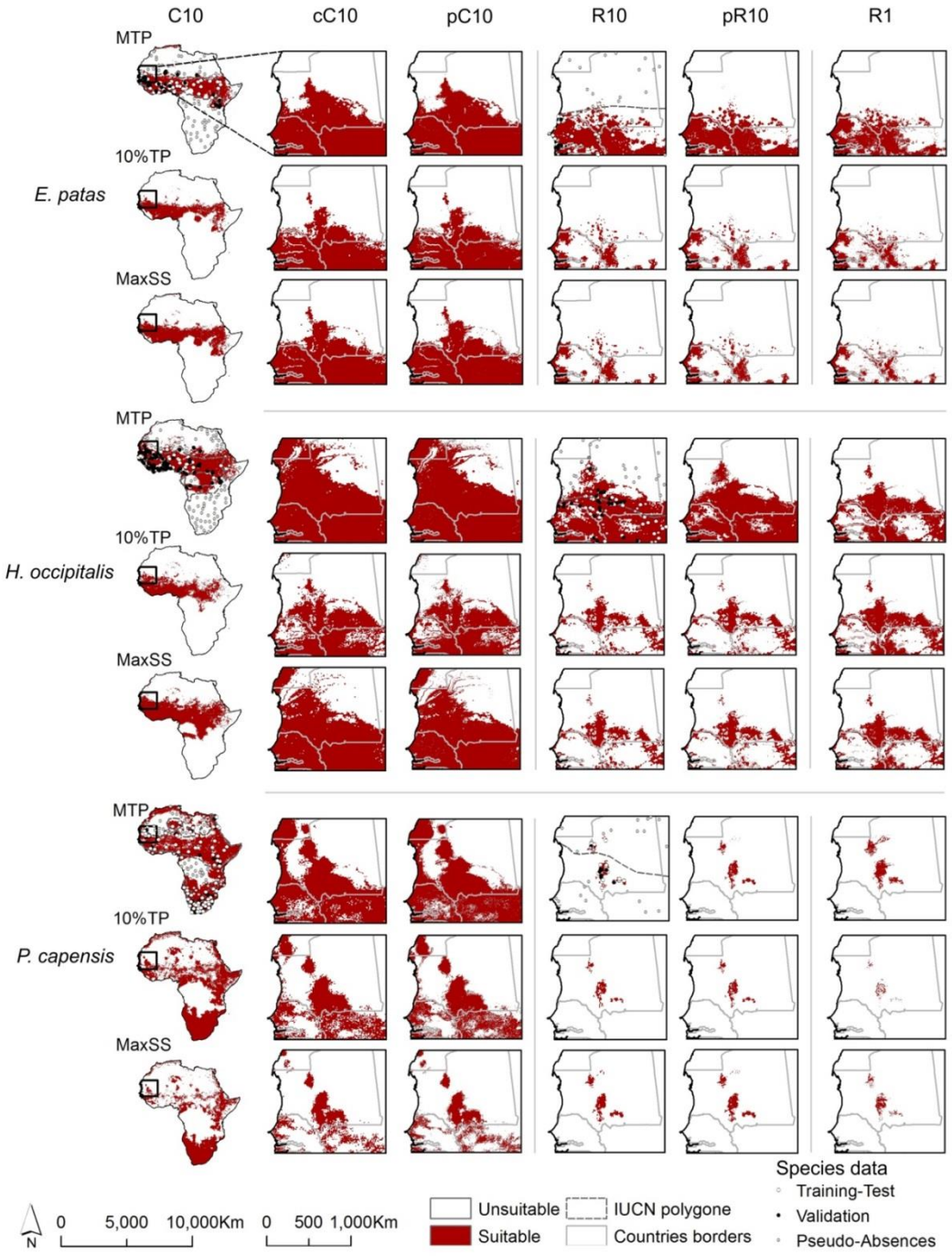

Fig. 3.6- Suitable areas for each target species predicted by each maximum entropy model type and projections according to three thresholds. From left to right: continental model at 10x10km (C10); West Africa extraction (cC10) from C10; projection of C10 into West Africa at 1x1km (pC10); regional model at 10x10km (R10); projection of R10 into West Africa at 1x1km (pR10); and regional model at 1x1km (R1). The thresholds used were: minimum training presences (MTP), 10th percentile training presence (10%TP), and maximum training sensitivity plus specificity (MaxSS).

Table 3.3 - Percentage of corrected classification of validation data (Val), absences (Abs), and the balance between them (Bal), of the target species according to the maximum entropy model types and three possible thresholds: minimum training presences (MTP), 10th percentile training presence (10%TP), and maximum training sensitivity plus specificity (MaxSS). Classification rates are given for models: continental at 10x10km (C10), regional at 10x10km and at 1x1km (R10 and R1, respectively), for projections C10 into West Africa at 1x1km (pC10) and R10 into West Africa at 1x1km (pR10), and for the West Africa extraction (C10 Clip) from the C10.

Threshold	Data	C10	cC10	pC10	R10	pR10	R1
	Erythrocebus patas						
	Val	100.0	100.0	100.0	100.0	100.0	100.0
MTP	Abs	96.8	38.2	38.2	73.5	70.6	73.5
	Bal	97.8	52.3	52.3	76.9	74.4	76.9
	Val	76.7	100.0	90.0	100.0	100.0	100.0
10%TP	Abs	98.4	50.0	55.9	85.3	85.3	85.3
	Bal	91.4	61.4	63.6	87.2	87.2	87.2
	Val	86.7	100.0	100.0	100.0	100.0	100.0
MaxSS	Abs	96.8	50.0	44.1	85.3	85.3	85.3
	Bal	93.5	61.4	56.8	87.2	87.2	87.2
	Hoplobatrachus occipitalis						
	Val	98.5	100.0	100.0	100.0	96.3	100.0
MTP	Abs	89.2	28.9	31.1	57.8	60.0	71.1
	Bal	93.3	46.7	48.3	73.6	73.6	81.9
	Val	83.6	93.3	93.3	88.9	85.2	96.3
10%TP	Abs	100.0	71.1	66.7	88.9	91.1	77.8
	Bal	92.7	76.7	73.3	88.9	88.9	84.7
	Val	94.0	100.0	100.0	88.9	85.2	96.3
MaxSS	Abs	97.6	44.4	44.4	88.9	91.1	80.0
	Bal	96.0	58.3	58.3	88.9	88.9	86.1
	Procavia capensis						
	Val	94.6	80.0	80.0	100.0	100.0	100.0
MTP	Abs	60.3	50.0	54.5	100.0	95.5	95.5
	Bal	72.4	55.6	59.3	100.0	96.8	96.8
	Val	89.2	80.0	80.0	100.0	100.0	100.0
10%TP	Abs	76.5	68.2	63.6	100.0	95.5	100.0
	Bal	81.0	70.4	66.7	100.0	96.8	100.0
	Val	78.4	80.0	80.0	100.0	100.0	100.0
MaxSS	Abs	86.8	77.3	81.8	95.5	90.9	95.5
	Bal	83.8	77.8	81.5	96.8	93.5	96.8

DISCUSSION

The choice of the appropriate study area extent, resolution and threshold for model classification are central issues in species distribution modelling (Wiens, 2002; Guisan & Thuiller; 2005, Liu *et al*., 2005; Guisan *et al*., 2007; Anderson & Raza, 2010). These choices have large impacts on model predictions, especially at edges of species distributions and they were addressed here, using two datasets for each species and training area (Africa and West Africa). Our results show that the study area extent, resolution of variables and the threshold choice led to differences in the performance and robustness of models to predicted species distributions at range margins.

THE EFFECTS OF USING COMPLETED OR RESTRICTED RANGE VARIABLES

Models calibrated with restricted environmental range are known to influence estimations of response curves (Thuiller *et al*., 2004; Barbet-Massin *et al*., 2010). As expected, we found different patterns in response curves between continental and regional model types: there was a trend for presence probability of all species to decrease abruptly in regional models (R10 and R1) and gradually in continental models (C10). Response curves illustrate the all-or-nothing character of suitable habitat availability in abrupt transition areas. This is the case of the Sahara-Sahel region, where the studied species are mostly restricted to suitable micro-habitats surrounded by large portions of unfavourable environmental conditions (Brito *et al*., 2010; Padial *et al*., *in press*). The most important variables were common at both scales for each species: distance to mosaics of cropland/vegetation for *E. patas*, and distance to *gueltas* to *P. capensis* and both variables to *H. occipitalis*. Our results also highlighted the importance of particular variables at regional scales in comparison to continental scales. For example, the relative importance of distance to *gueltas* for *P. capensis* was higher in regional than in continental models. On the contrary, the importance of the most important variables to explain distribution of species in regional models appeared to be less relevant amongst others factors in continental models. Our results support the view that at range margins of species distribution, where availability of optimal habitats is limited, species are forced to occupy suboptimal habitats different from global mean (Braunisch *et al*., 2008). Marginal populations may have local adaptations to climatic conditions that are distinct from the conditions across the species global range (Trivedi *et al*., 2008). ENFA indicated a strong tendency for all species to select particular habitats in regional than in continental scale models, the

latter overestimating predicted suitable areas (Fig. 3.3). These results also support that widespread species may show regional ecological adaptations, resulting in different habitat preferences in discrete parts of the species' range (Stockwell & Peterson 2002). When the complete range of widespread species is modelled, differences in ecological preferences between subpopulations may lead to reduced model accuracy and overestimation of species' ecological breadth at range margins (Stockwell & Peterson, 2002; Hernandez *et al*., 2006).

THE EFFECTS OF USING EXTENSIVE OR RESTRICTED PRESENCE DATA

Predictions of species distribution differed when we used complete or restricted presence datasets. The continuous probability of occurrence associated with each pixel and the range and shape of the predicted suitable area for each species varied between distinct spatial extents. Overall, continental models adjusted to species' occurrence data, which supports that ENMs perform well with extensive presence data (Barbet-Massin *et al*., 2010). However, when we focus on the range margin, continental models tended to overestimate species distribution (cC10, Fig. 3.6), while regional models tended to adjust better to presence data (R10 and R1; Fig. 3.6). Differences between continental and regional model predictions have been observed in macro-scale models for mountain plant species that performed well across Europe and overestimated areas of occupancy within Britain (Trivedi *et al*. 2008). In fact, small study regions led to more realistic estimates of species' potential distributions when compared with larger areas (Anderson & Raza 2010), given that at range margins, the most suitable habitats present in core range areas become scarcer and species may occupy suboptimal habitats that otherwise would be discarded. Moreover, ENMs based on the absolute environmental range may generalise predictions to local unsuitable areas (Braunisch *et al*., 2008; Trivedi *et al*., 2008). In comparison to continental models, regional predictions provided more detailed spatial distributions, which allowed detecting isolated micro-habitats. For instance, in West Africa *P. capensis* is restricted to mountains and areas in proximity of *gueltas*, and this pattern could only be detected in regional models. Thus, at a regional scale, local models should be preferred over continental models, since the former gave more detailed predictions of suitable areas that could optimise reserve design approaches for local-scale conservation planning.

THE EFFECTS OF RESOLUTION

Predicted distributions of species varied between different resolutions (10x10km and 1x1km) and especially, when different extents for training models were used. Overall, continental models at coarse resolution (C10) showed a good level of agreement with species' occurrence data. However, zooming at the edge of range (cC10), they tended to overestimate species distributions, as observed by the low correct classification rates of absence data in comparison to validation data. In fact, continental models tend to be ambiguous at range margins, failing to detect isolated small patches or local and fragmented distributions (Fjeldså & Tushabe, 2005). Models calibrated using coarser resolutions may substantially overestimate potentially suitable areas in comparison to those built with finer resolution data (Wiens *et al*., 2009). The accuracy and spatial output agreement of continental distribution maps tends to decline when grid size increases (Guisan *et al*., 2007; Seo *et al*., 2009; Wiens *et al*., 2009). Nevertheless, when models were calibrated in West Africa, differences between resolutions were less evident, which agrees with previous findings of no effects of pixel size on regional model performance (Guisan *et al*., 2007; Trivedi *et al*. 2008). Moreover, the range extent and configuration of predicted distributions at local scale differed between projections from continental and regional models (pC10 and pR10). Continental models built with coarse resolution projected into regional at 1x1km (pC10) tended to overestimate species distribution. Inaccuracy in the projection of coarse models to local fine scales has been observed in plant species models built at 10x10km and projected to 2x2km resolution (Collingham *et al*., 2000). Indeed, downscaling processes require that one of the two effects, spatial extent or resolution, must be held constant, and therefore projections from large to small extents is appropriate if data resolution is held constant (Collingham *et al*., 2000; Trivedi *et al*., 2008). On the other hand, the projection of regional models from 10x10km to 1x1km fitted to presence data, which further supports the notion that models can be downscaled to predict local distributions from coarse-resolution data (Barbosa *et al*., 2010). Our results also suggest that projections from coarser to finer resolutions are applicable if study area extents are constant, but decreasing resolution limits the detection of suitable habitat patches. For regional and local conservation planning, models with high resolution data should be applied to define quality areas for the application of concrete conservation measures (Collingham *et al*., 2000; Trivedi *et al*., 2008, Seo *et al*., 2009; Jiménez-Alfaro *et al*., 2012). However, the limited availability of high resolution data precludes its frequent use and in this context, downscaled models may constitute an alternative

way to identify suitable areas for conservation actions and areas where local distribution data cannot be achieved (Araújo *et al*., 2005; Barbosa *et al*., 2010).

THE EFFECTS OF THRESHOLD SELECTION FOR MODEL CLASSIFICATION

The importance of threshold selection appears to change between model extents. At continental extent, the accuracy of predicted suitable areas was more dependent on the threshold used than at regional scale, especially when zooming to the edges of species distributions (cC10, Fig. 3.6). Using native tree species distributed across Europe and projections for future climates, Nenzén & Araújo (2011) also pointed out that in large study areas with extended climate gradients, models tend to perform well but threshold choice contributes to more uncertainty. However, at range margins, the accuracy of predicted suitable areas increased with increasingly restrictive thresholds. Given that the appropriate threshold for detecting species presence tends to decrease as species distribution becomes more sparse (Collingham *et al*., 2000), more restrictive thresholds tended to increase the balance between the percentage of correct classification of both validation data and absences in the cC10. The influence of data sparseness in threshold selection was also observed in regional models, despite the fact that all thresholds used tended to fit presence data reasonably well, which further supports that an optimal threshold is more difficult to discern with limited data (Bean *et al*., 2012). For both R10 and R1, the optimum threshold was the tenth percentile training presence (10%TP) followed by the maximum training sensitivity plus specificity threshold (MaxSS). Given that at range margins of species distributions, species are generally limited to fragmented habitats, more restrictive thresholds increased the balance between correct classification of both validation data and absences, although maximizing the fraction of true positives (Liu *et al*., 2005; Jiménez-Valverde & Lobo, 2007; Raes *et al*., 2009; Braunisch & Suchant, 2010). Nevertheless, when models were calibrated at regional scale, the accuracy of predicted suitable areas was independent of the threshold used. Thus, its selection seemed only dependent on the study goals. For example, while establishing protected areas, it may be more appropriate to use a less restrictive threshold (Liu *et al*., 2005), such as the minimum training threshold (MTP).

CONCLUSIONS

In range margins of species distributions, especially those located in abrupt climatic and/or habitat transition zones, species tend to select particular habitats and live in narrow conditions, in comparison to the core of species distribution. Our results show that models calibrated in the regional area with restricted and high resolution data outperform projections of coarse scale models built using the absolute range of distribution to the regional area. For local conservation planning and especially to identify optimal surveys sites under present conditions, models calibrated with fine resolution should be applied instead of coarse resolution data. However, fine resolution data cannot always be collected and thus downscaled models within the same area extent could be a valid alternative. When models were built at regional scale using precise data, less restrictive thresholds that minimise the omission error may be used, depending on the study goals. Therefore, regional models built with precise data and conservative thresholds could be the most cost-effective option for defining accurate ranges and effective designs for protected areas at range margins of species distributions.

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ARTICLE II. APPLYING SPECIES DISTRIBUTION MODELLING TO THE CONSERVATION OF ANECOLOGICALLY PLASTIC SPECIES (*PAPIO PAPIO*) ACROSS BIOGEOGRAPHIC REGIONSIN WEST AFRICA[2]

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ABSTRACT

Ecological niche models are valuable tools to support conservation decision-making. Still, they are sensitive to the study area spatial extent. Ecologically plastic species ranging over different biogeographic regions often exhibit populations adapted to distinct environmental conditions. In such cases, regional models may be more accurate than global models in discriminating suitable areas in specific regions under such circumstances. We use the Guinea baboon as model system, to test the effects of restricting the range of environmental variables and study area extent, and explore geographic differences in the environmental conditions occupied by ecologically plastic species. Additionally, we explore conservation implications for this particular case study. We built global (West Africa) and regional models (Sahel, Savannah and Afrotropical) using a maximum entropy approach and explore geographic differences in environmental conditions occupied by regional populations using Principal Components Analyses. The most important variables identified differed between model types, distance to gueltas in global model and distances to gueltas, to croplands and to water bodies in regional models, as well as models' accuracy to define distribution and suitable areas, which are overestimated by global models. Environmental conditions overlapped slightly between regional populations, and the Sahel displayed the most divergent one. Areas of potential conflict between the species and humans were identified in the Savannah and Afrotropical region, but latter lack protected areas. We show for modelling the current distribution of ecologically plastic species, regional models are more accurate than global models in defining the species' environmental predictors and suitable areas. This will improve the definition of accurate local suitable areas for ecologically plastic species and improve the allocation of resources for local conservation actions.

Keywords: Ecological niche models; global models; Guinea baboon; regional models; spatial extent; Sahel

INTRODUCTION

Defining priority areas for conservation is a major goal of biodiversity conservation (Jenkins, Pimm, & Joppa, 2013). Ecological niche models (ENMs) can greatly improve decision-making in conservation management, in particular, when the ecological knowledge is incomplete (Elith & Leathwick 2009a; Addison *et al*., 2013). In the last years, ENMs have become widely applied in several disciplines, including conservation assessments (Doko, Fukui, Kooiman, Toxopeus, & Ichinose, 2011; Addison *et al*., 2013; Bosso, Rebelo, Garonna, & Russo, 2013; Guisan *et al*., 2013; Virkkala, Heikkinen, Fronzek, & Leikola, 2013; Russo *et al*., 2014). However, ENMs are also subject to uncertainty, requiring numerous methodological and well-justified decisions. Among others, ENMs are sensitive to a number of scale-related issues (Guisan, Graham, Elith, & Huettmann, 2007), such as the spatial extent of the study area (Elith & Leathwick, 2009b; Franklin & Miller, 2009), which is also a key factor affecting conservation planning (Hermoso &Kennard, 2012). In ENMs, the use of occurrence data from the complete species distribution range or at least from within complete biogeographical areas is recommended (Barbet-Massin, Thuiller, & Jiguet, 2010). The inclusion of the complete species' environmental range in ENMs is considered the best strategy to predict species environment interactions for different regions or time periods from where the models were built (Thuiller, Brotons, Araújo, & Lavorel, 2004; Barbet-Massin *et al*., 2010; Russo *et al*., 2014).

Broad-scale and multi-country assessments outperform local scale studies in terms of conservation efficiency (Hermoso & Kennard, 2012). However, practical conservation actions often unfold on a regional or local geographical scale, and more frequently, within political boundaries (Elith & Leathwick, 2009a; Hermoso & Kennard, 2012). At fine scales, abiotic or biotic factors rather than climate itself could shape the species distribution (Elith & Leathwick, 2009b; Wiens & Bachelet, 2009). At this level, ENMs applied to conservation planning are expected to discriminate not only the broad area of species' occurrence but also to distinguish areas more suitable than others (Elith & Leathwick, 2009a; Doko *et al*., 2011; Bosso *et al*., 2013). For ecologically plastic species, whose populations may be adapted to distinct local environmental conditions within the species' range, the discriminatory ability of ENMs could be limited (Peterson, 2003). Past studies showed specialist species or species with limited geographical extent yielded more accurate models than generalists or species with wide geographical ranges (Segurado & Araújo, 2004; Buisson, Thuiller, Casajus, Lek, & Grenouillet, 2010). A further scrutiny of these results showed they might be related to

the spatial extent of the analysis (Elith *et al*., 2006), raising the questions if a constant extent of analysis is appropriate for all species in relation to the purpose of the predictions (Elith *et al*., 2006) and if models built with the entire species range are suitable to identify fine scale patterns of distribution. Furthermore, the ecological and biogeographic context may affect model performance (Osborne & Suárez-Seoane, 2002; Suárez-Seoane, Virgós, Terroba, Pardavila, & Barea-Azcón, 2014). Generally, species tend to be more abundant at the ecological core of their distribution and become rare and specialized as the availability of environmental conditions decreases and/or become more extreme (Brown, Mehlman, & Stevens, 1995). The performance of the models can be biased for species ranging over different biogeographical areas and for populations inhabiting the most distinct environments at the extremes of the range, which may deserve particular local conservation assessments considering their rarity.

The Guinea baboon (*Papio papio*, Desmarest 1820) displays high ecological plasticity and occupies different biogeographical areas throughout its range. The species' range follows a latitudinal gradient in precipitation: from arid conditions in the Sahel to secondary forest in the Afrotropical biogeographic area. Considering the Near Threatened status (Oates, Gippoliti, & Groves, 2008), Guinea baboons are in need of specific conservation measures indistinct locations. In both West Sudanian Savanna and Afrotropical biogeographic areas, range contraction and population fragmentation have been related to agricultural expansion and hunting for meat and pet trade (Oates *et al*., 2008; Ferreira da Silva, 2012; Ferreira da Silva, Godinho, Casanova, Minhós, Sá, & Bruford, 2014).While in the Sahel there are no evidences of range contraction, particularly associated with human activities. Yet populations were mainly observed in mountain rock-pools (locally known as gueltas, Cooper, Shine, McCanna, & Tidane, 2006; Brito, Alvares, Martínez-Freiría, Sierra, Sillero, & Tarroso, 2010), suggesting a tight association between species occurrence and water availability. Distinct environmental and human-related pressures could shape Guinea baboon distribution in different biogeographical areas but the relative contribution of each factor across areas is unknown. For this this highly plastic species, global models can be less accurate than regional models in defining suitable areas. High accuracy mapping of suitable areas is needed for the identification of potential areas of conflict with humans, and for estimating range fragmentation levels and the number and location of subpopulations. Such knowledge is basal to identify potential conservation units and define priorities for species conservation at the local level.

In this work, we aim to assess how the performance of global and regional models affects predictions of the distribution of ecological plastic species. We used as model

system the Guinea baboon and we addressed three specific questions: (1) Does the importance of variables for the species occurrence differ across biogeographic areas? (2) Does the performance of models for identifying suitable areas for the species occurrence differ in distinct biogeographic areas? (3) Is there niche overlap between suitable areas predicted by regional models? According to the above referred evidences, we expected: the most important environmental variables related with the species' distributions to differ between biogeographic areas; regional models to perform more accurately in defining suitable areas and; discordance between predicted suitable areas in each ecoregion. Additionally, we identified isolated subpopulations, potential areas of conflict with human activities and degree of formal protection of predicted suitable areas to inform local conservation planning of Guinea baboons. We expect to demonstrate that when working with ecologically plastic species, local-scale studies could be more accurate to define local suitable areas and that local models may outperform broad-scale assessments in terms of conservation efficiency.

MATERIALS AND METHODS

TRAINING AREAS

We selected four areas for model training: West Africa and three restricted areas (Sahel, Savannah and Afrotropical), which match with the global and regional scales, respectively (Fig. 3.7). West Africa was delimitated with both a buffer of 150 km bounding the IUCN polygon of the species distribution (Oates *et al*., 2008) and the observation data (Fig. 3.7). Regional areas correspond to three major biogeographic areas and were accessed by WWF terrestrial ecoregions (Olson *et al*., 2001): Sahelian Acacia Savanna (Sahel) and West Sudanian Savanna (Savanna) ecoregions, and the Afrotropical, comprising the Guinean forest-savannah mosaics, Guinean mangrove, Guinean montane forest and the Western Guinean lowland forest ecoregions, all included in the Afrotropical biogeographic realm (Fig. 3.7).

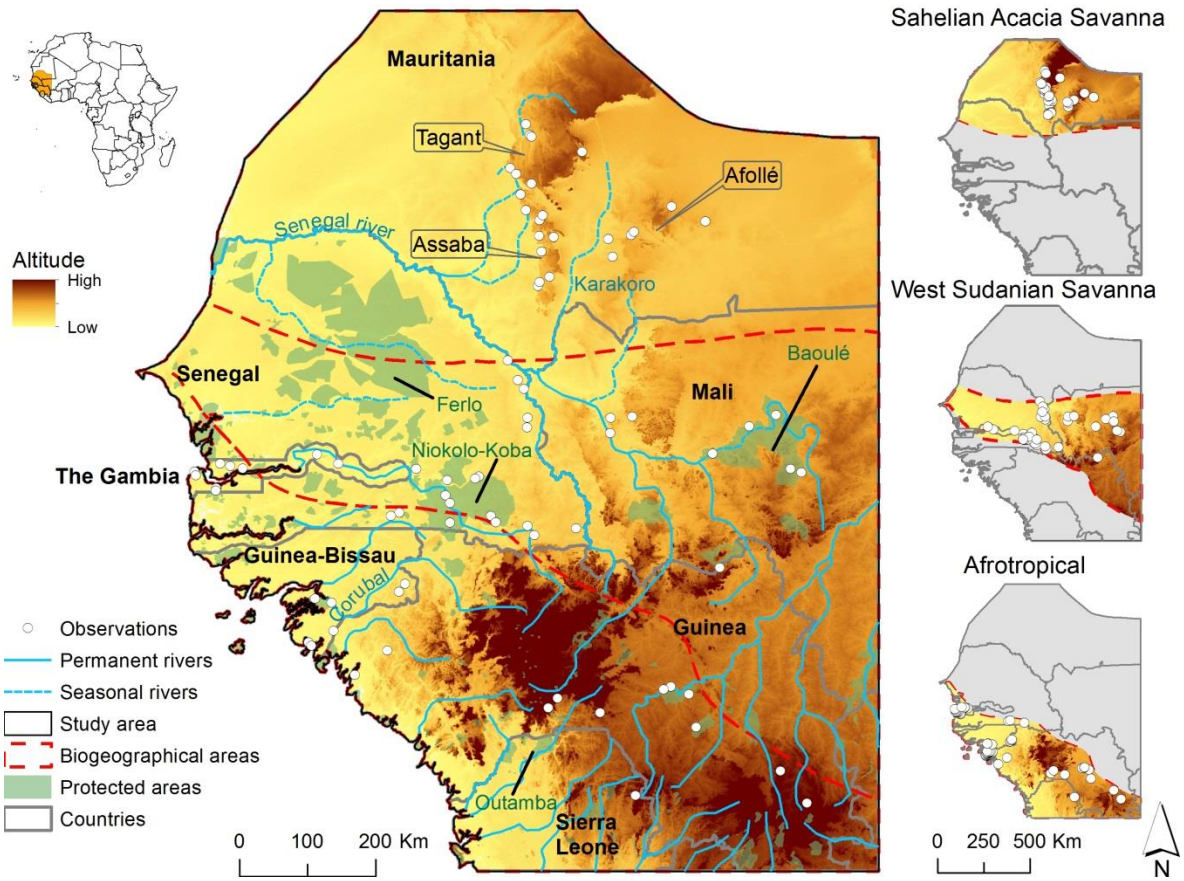

Fig. 3.7- Study area and distribution data of *Papio papio* in each training area: West Africa (left), Sahelian Acacia Savanna, West Sudanian Savanna and Afrotropical training areas, and location of West Africa in African context (small inset). River names are given in blue and mountain names in grey boxes. Major national parks names are indicated in green.

PRESENCE DATA

As model system, we used the Guinea baboon. We assembled141 geo-referenced observations of the species and they were used for modelling purposes (Fig. 3.7): 75 were collect by the authors using a Global Positioning System (GPS) (Torres 2007; Brito *et al*., 2010; Ferreira da Silva *et al*., 2014), and 66 bibliographic observations (see Supplementary material Appendix B.1), including geo-referenced localities or clear toponomies from which coordinates were collected with 1 km precision. For West Africa dataset, we randomly selected a total 79 non-clustered observations from clusters of species occurrence according to the Nearest Neighbour Index (NNI) estimated using ArcGIS 10.0 (ESRI, 2011) and two datasets were built: 50 observations for training and testing and 29 observations for the validation dataset (see Supplementary material Appendix B, Table B.1). We divided the initial dataset according to each regional training area and repeated the previous procedure (Sahel:

N = 35; savannah: N = 41; afrotropical: N = 46; see Supplementary material Appendix B, Table B.1). Following the same approach, for each training area, from total number of observations two datasets were built, one for training and testing models and another for validation (see Supplementary material Appendix B, Table B.1).

ECOGEOGRAPHICAL VARIABLES

We used the same set of 14 ecogeographical variables (EGV) in all training areas. All EGVs were re-projected from WGS84 datum to WGS 1984 UTM Zone 28N. EGVs included one topographical grid (USGS 2006) used to derive Slope, using 'Slope' function of ArcGIS; four climate grids (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005); seven distances to habitats grids derived from a land-cover grid for the years 2004–2006 (Bicheron *et al*., 2008), and distance to permanent and seasonal gueltas, both digitized from the IGN maps and ground-validated in Mauritania by fieldwork (Table 3.4). To convert the original categorical habitat EGVs (including gueltas) into continuous variables, we created one binary grid for each habitat type. We calculated the Euclidean distance of each grid cell to the closest habitat type cell. All EGVs had 30" pixel size (~1 km). Most EGVs had correlation coefficients below 0.77 but higher correlations between some EGVs were allowed, namely distance to permanent and to seasonal gueltas (0.98), and both with annual mean temperature(0.80 and 0.81, respectively), given the likely importance for the ecology and distribution of the species (Cooper *et al*., 2006; Brito *et al*., 2010).

Table 3.4 - Description, range (minimum and maximum), and units of environmental factors used for modelling the distribution of *Papio papio* in West Africa (WA), and in the Sahelian Acacia Savanna (SAS), West Sudanian Savanna (WSS) and Afrotropical (AFR) biogeographical areas.

Code	Description	Units	Range			
			WA	SAS	WSS	AFR
ATEM	Annual average temperature	º C	18.0 - 30.8	24.4-30.8	23.4 - 30.1	18.0 - 30.5
MTEM	Minimum temperature of coldest month	º C	8.7 - 23.0	11.9 - 17.2	10.3 - 18.9	8.7 - 23.0
PWET	Annual average total precipitation of wettest month	mm	27 - 1195	27 - 223	127 - 394	195 - 1195
PET	Annual average potential evapo-transpiration	mm	1252 - 2246	1536 - 2206	1333 - 2246	1252 - 2203
SLOP	Slope	%	0 - 53	0 - 28	0 - 31	0 - 53
	Distance to:					
CROP	Croplands	º	0 - 2.98	0 - 2.24	0 - 1.95	0 - 2.98
VECR	Mosaic vegetation/cropland	º	0 - 2.21	0 - 2.21	0 - 0.77	0 - 0.54
COSH	Closed to open shrubland	º	0 - 2.94	0 - 2.94	0 - 0.48	0 - 0.47
COHE	Closed to open herbaceous vegetation	º	0 - 3.50	0 - 0.81	0 - 3.14	0 - 3.50
FBWV	Freshwater or brackish water vegetation	º	0 - 3.98	0 - 3.71	0 - 3.98	0 - 2.79
BARE	Bare areas	º	0 - 1.30	0 - 0.90	0 - 1.30	0 - 1.10
WABO	Water bodies	º	0 - 2.87	0 - 2.87	0 - 1.87	0 - 1.79
PERM	Permanente *gueltas*	º	0 - 8.99	0 - 4.15	0.98 - 8.11	3.18 - 8.99
SEAS	Seasonal *gueltas*	º	0 - 8.61	0 - 4.57	1.29 - 7.69	3.59 - 8.61

MODELLING STRATEGY

Our analysis was done at two spatial scales: global (West Africa) including complete species environmental range and regional that corresponded to each biogeographic area (Sahel, Savannah and Afrotropical). To identify EGVs related to species' distribution and to derive models of species probability of occurrence in all training areas, we used the Maximum Entropy approach implemented in Maxent 3.0.4 beta (Phillips, Anderson, & Schapired, 2006). This technique requires only presence data as input and consistently performs better than other methods (Elith *et al*., 2006; Hernandez, Graham, Master, & Albert, 2006). We developed four models using distinct training areas (West Africa and Sahel, Savannah and Afrotropical models). Each model type was built with random seed and 10 replicates, with 10% of test data chosen by bootstrap with random seed, auto-features, and logistic output (Phillips *et al*., 2006). Area under the curve (AUC) of the receiver-operating characteristics (ROC) plot was taken as a measure of the models fitness (Fielding & Bell, 1997). We averaged the 10 replicates to generate a forecast of species presence probability, which is a robust procedure to derive consensus predictions of species likelihood of presence (Marmion, Parviainen, Luoto, Heikkinen, &Thuiller, 2009).

We determined the EGVs' importance for explaining the species' distribution from their average percentage of contribution and permutation importance to each model type and their average gain with training and test data using a Jackknife analysis. We determined the relationship between species' occurrence and EGVs by visual examination of response curves profiles from univariate models.

We reclassified all training models to display areas of probable presence and absence for the species. We used the maximum training sensitivity plus specificity threshold (MaxSS) because conservative thresholds could be the most cost-effective option for defining accurate ranges at regional scales (Vale, Tarroso, & Brito, 2014). Additionally, it minimizes omission and commission error sand is appropriate when only presence data is available (Liu, Berry, Dawson, & Pearson, 2005; Liu, Soininen, Han, & Declerck, 2013).The best cut-off value corresponds to the point where sensitivity and specificity are maximized on the ROC curve (Braunisch &Suchant, 2010). To calculate MaxSS, we firstly randomly generated four pseudo-absence datasets in ArcGIS for each training area with the same number of observations used in the training datasets. Pseudo-absences likely correspond to true absences, because they were created at a distance of at least 100 km from the presence data. The buffer size was set taking into account the species home range (about 25 km2, Dunbar, 1988) and the daily-distance covered (>40 km; Galat-Luong personal communication, in Ferreira da Silva, 2012).

Both the model training observations and the pseudo-absence datasets were intersected with the average probability of occurrence model. The point of intersection of both observations curves was taken as the MaxSS.

We combined the Sahel, Savannah, and Afrotropical models in one single binary prediction (Combined model) and overlapped it with the West Africa model to compare between accuracy of regional and global models. We validated all binary maps by calculating the correct classification rates (CCR) of the validation and pseudo-absence dataset, the overall accuracy, sensitivity, specificity and both Kappa and TSS statistics. To allow comparing the predictions of regional models with the WA model, we have broken down the WA predictions and calculated the above statistics for each biogeographic area. To calculate CCRs of data, we intersected both validation and pseudo-absences datasets with each training model. Overall accuracy, sensitivity, specificity, Kappa statistic and True Skills Statistic (TSS) were calculated for all models by applying each statistics to a 2 × 2 confusion matrix. Overall accuracy is the proportion of correctly predicted observations. Kappa statistics corrects the overall accuracy of model predictions by the accuracy expected to occur by chance. Sensitivity is the probability that models will correctly classify a presence, while specificity is the probability that models will correctly classify an absence. For the confusion matrix, TSS = sensitivity + specificity − 1 (see, Allouche, Steinitz, Rotem, Rosenfeld, & Kadmon, 2006).

NICHE OVERLAP ANALYSIS

We measured the similarities between the predicted habitat suitability for populations in each biogeographic area (Sahel, Savannah, and Afrotropical) and between the predicted species niche in the West Africa and the Combined models. The niche overlap was measured by two different statistics—Schoener's D (Schoener1968) and I, using ENMTools (Warren, Glor, & Turelli, 2008, 2010), which range from 0 to 1 when species/populations have completely discordant or identical ENMs, respectively.

Spatial environmental data of each biogeographic area and predicted by West Africa model was summarized by a Spatial Principal Components Analysis (SPCA) in three orthogonal components. Environmental data was previously centred and scaled due to different measurement units. The spatial environmental range of the West Africa model was visually compared with the retained components of each of the biogeographic areas.

CONSERVATION-RELATED PARAMETERS

Suitable areas predicted by the most accurate model were intersected with a human population density raster to identify potential areas of conflict. Human population density to the year2000 (CIESIN & CIAT, 2005) was reclassified into three groups: low (<5 people/km2), medium (5–50 people/km2) and high (>50people/km2). Suitable areas were intersected with a shapefile of implemented protected areas (IUCN & UNEP, 2013) to quantify the percentage of formally protected suitable areas.

Number of subpopulations was quantified based on suitable isolated patches forecasted by the most accurate model. We considered a subpopulation when distances between suitable isolated patches exceeded 50 km. Although the dispersal ability of the species is unknown, the threshold used accounting for the home range and the daily distance covered per day (see above).

RESULTS

ROC plots exhibited high average AUCs for both training and test datasets for all model types. Average AUCs ranged from 0.92 to1.00 between different model types for training datasets and from 0.81 to 0.99 for test dataset (see Appendix B, Table B.2).

IMPORTANCE OF ENVIRONMENTAL FACTORS

Percentage of contribution, permutation importance, and Jackknife evaluation identified identical EGVs most related with species distribution in Sahel, Savannah, Afrotropical and West Africa models but not between them (Fig. 3.8 and Appendix B Table B.3). Both West Africa and Sahel models identified distance to permanent and seasonal gueltas as the most important EGVs related with the species distribution. Both distance to permanent gueltas and to croplands were the most important EGVs in the Savannah model, and distance to water bodies and to croplands, in the Afrotropical model (Fig. 3.8 and Appendix B Table B.3). All jackknife results suggested that distance to permanent and seasonal gueltas had a disproportional importance for the West Africa and Sahel models, while for the Savannah and Afrotropical models, the relative importance of EGVs changed according to training, test and AUC gain (Fig. 3.8 and Appendix B Table B.3).

The response curves profiles of the shared EGVs exhibited different pattern between global and regional modes (Fig 3.9). For instance, the species presence probability decreased abruptly within creasing distance to both seasonal and permanent gueltas

in the Sahel model. In the West Africa model, it started by decreasing but increased as distance to both variables increase (Fig. 3.9). A similar pattern was observed for distance to seasonal gueltas in the Savannah model.

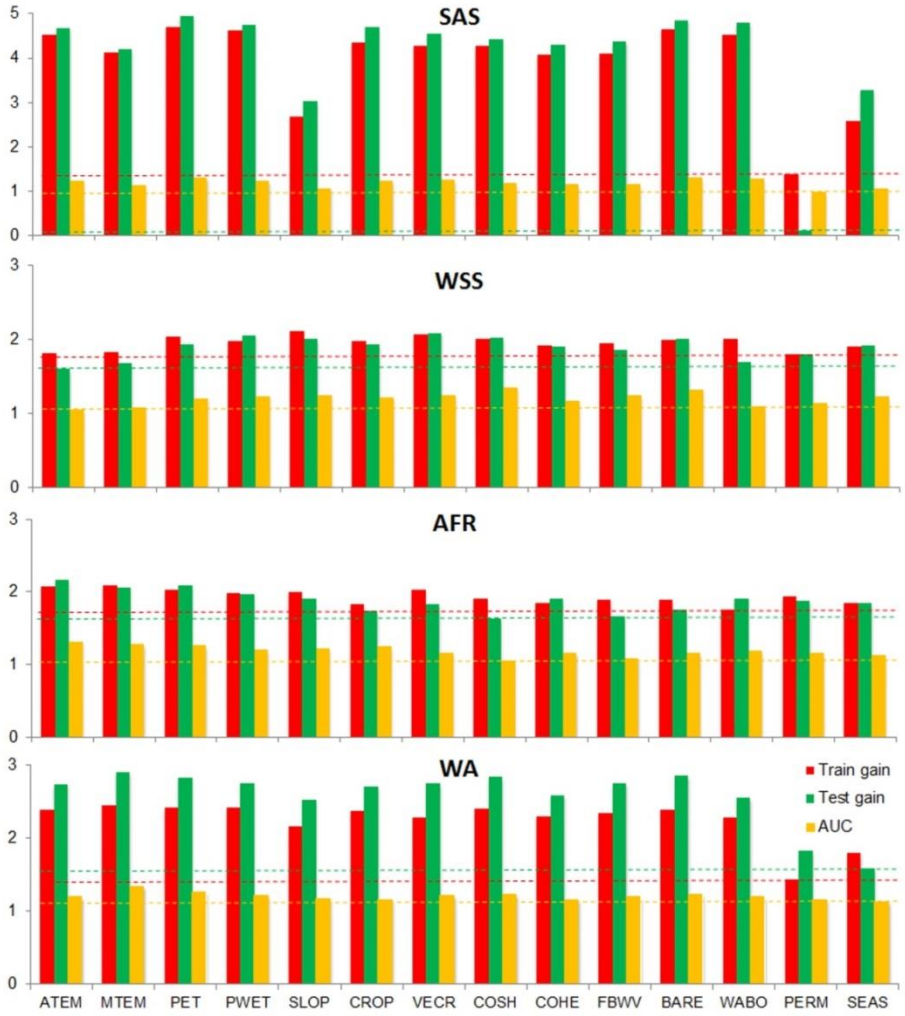

Fig. 3.8- Jackknife results for the environmental factors used in each maximum entropy model type. For each variable, difference in average gain between models built without a given variable and models built with only that variable using training and test data are presented. Variables with lower differences are the ones most related to species distribution. Explanation of variable codes is given in Table 1. Red, green and yellow dash lines are guidelines for visualization of the important environmental factors according to the training, test and AUC gain differences. From top: Sahelian Acacia Savanna (SAS), West Sudanian Savanna (WSS), Afrotropical (AFR) and West Africa (WA) model.

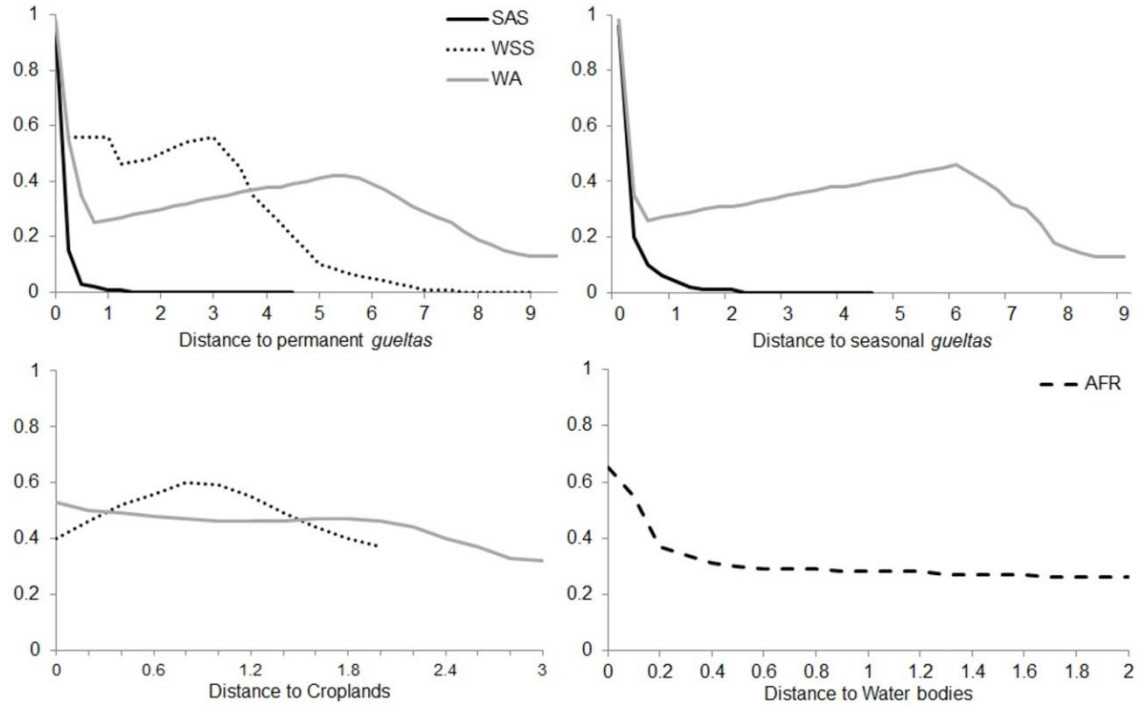

Fig. 3.9- Response curves for the environmental factors most related to the distribution of *Papio papio* in each Maxent model type: West Africa (WA), and the Sahelian AcaciaSavanna (SAS), West Sudanian Savanna (WSS), and Afrotropical (AFR).

MODEL COMPARISON

Overall, all model types predicted suitable areas in the same locations within biogeographical areas but the range and configuration of those areas were different (Fig. 3.10a). Both global and regional models (Sahel, Savannah and Afrotropical) fitted to the species' occurrence data. Overall, measures of the predicted accuracy for regional models were equal or higher than for global models when analysing results for a specific biogeographical area, with one single exception: sensitivity in WSS (Table 3.5). The same pattern was observed when comparing the combined model directly with the WA model (Table 3.5). Correct classification rates (CCR) of the training and validation datasets were higher in the global model whereas CCR of the pseudo-absence datasets was higher for regional models. The overlap map showed agreement areas by both models (48.6%; Fig. 3.10). The West Africa model tended to over-estimate suitable areas (42.6% more), while the Combined model was more accurate (Fig. 3.10). This difference was also observed in the higher values of CCRs pseudo-absences in the combined model (Table 3.5).

Table 3.5 - Measures of predictive accuracy calculated from a 2×2 error matrix. Sensitivity and Specificity are the probability that the model will correctly classify a presence and an absence, respectively. Kappa and True Skill Statistic (TSS) normalize the overall accuracy by the accuracy that might have occurred by chance alone. Overall accuracy is the rate of correctly classified cells. Percentage of correct classification of absence data (CCR Abs); training data (CCR train) and validation data (CCR Valid). Measures were calculated for all possible maximum entropy model types: West Africa (WA), Sahelian Acacia Savanna (SAS), West Sudanian Savanna (WSS), Afrotropical (AFR), and Combined model. The results for the combined model are presented for each biogeographic area: Sahelian Acacia Savanna (WA_{SAS}); West Sudanian Savanna (WA_{WSS}) and Afrotropical (WA_{AFR}).

Models	**SAS**	**WSS**	**AFR**	**Combined**	**WA**	**WA_{SAs}**	**WA_{WSS}**	**WA_{AFR}**
Sensitivity	1.0	0.9	1.0	0.9	1.00	1.0	1.0	0.9
Specificity	1.0	0.9	1.0	1.0	0.9	1.0	0.8	0.7
Kappa	1.0	0.8	0.9	0.9	0.8	1.0	0.8	0.6
TSS	1.0	0.8	0.9	0.9	0.8	1.0	0.8	0.6
Overall Accuracy	1.0	0.9	1.0	1.0	0.9	1.0	0.9	0.8
CCR Abs	100	91.3	96.3	98.0	86.0	100	82.6	70.4
CCR Train	96.3	91.3	96.3	92.0	96.0	100	100	88.9
CCR Valid	87.5	94.4	84.2	86.2	86.2	100	94.4	89.5

NICHE OVERLAP ANALYSIS

Niche overlap analysis predicted more similar environmental conditions of the populations in adjacent biogeographic areas (see Appendix B Table B.4). Predicted suitable areas for the populations in the Sahel are the most discordant in I and D statistics (see Supplementary material Appendix B Table B.4). Niche-overlap analysis between the predicted suitable area sin West Africa and the Combined models did not significantly reject the hypotheses of similarity and discordance (see Supplementary material Appendix B Table B.4).

The first three axes of SPCA explained 66.8% of environmental variability of the West Africa study area (Fig. 3.11). There was little overlap in environmental ranges of the biogeographic areas (Fig. 3.11). The distribution of the environmental variability of the West Africa model overlapped with all biogeographic areas (Fig. 3.11).

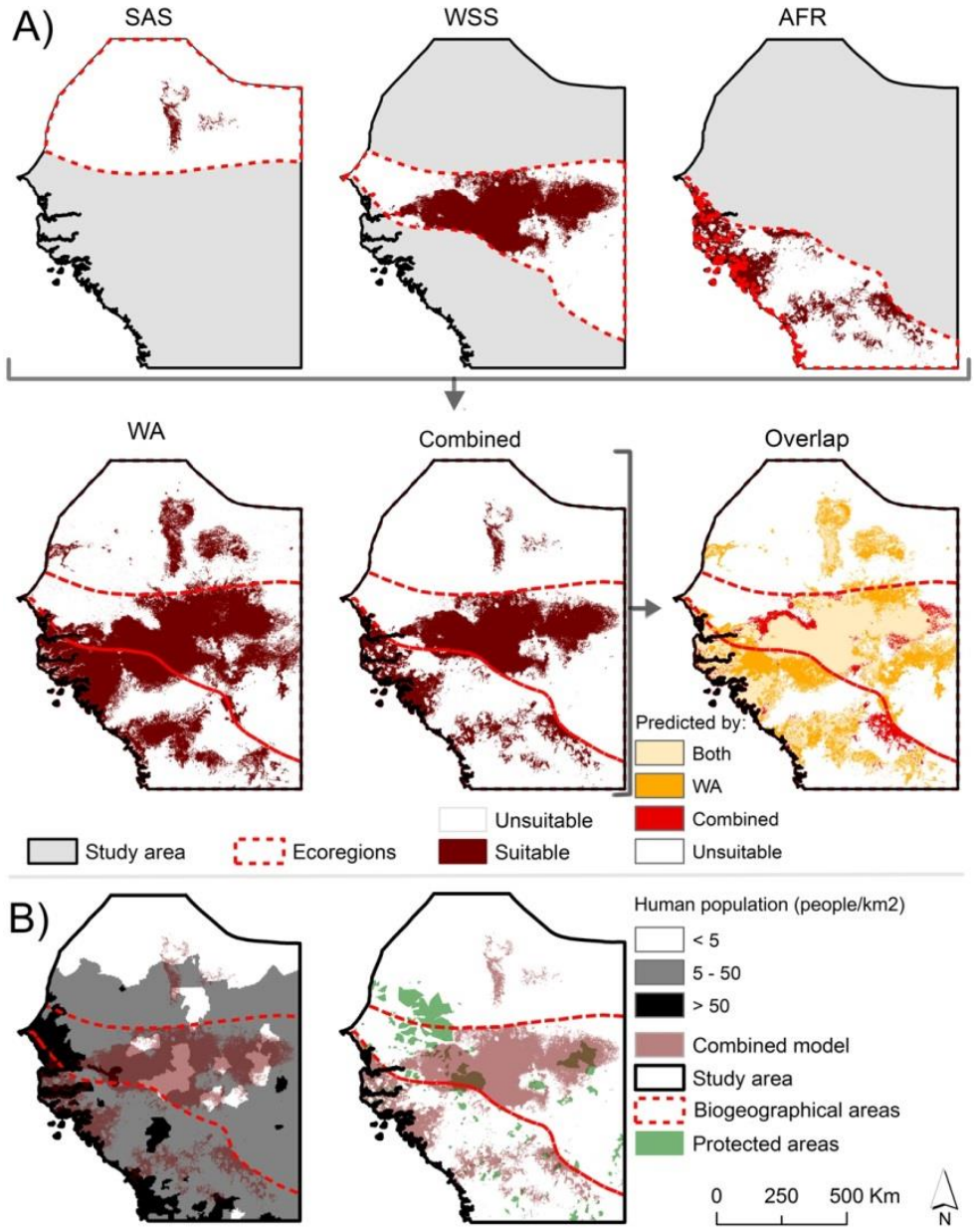

Fig. 3.10- Predicted suitability areas for *Papio papio* by each model type. (A) Predicted suitable areas by each maximum entropy model type. At the top, from left to right: Sahelian Acacia Savanna (SAS), West Sudanian Savanna (WSS) and Afrotropical (AFR) models. In the second line, from the left to right, the West Africa (WA) model, the Combined model (SAS + WSS + AFR) and the overlap between both. (B) From the left to right, overlap between combined model with human population density (people/km2) and protected areas.

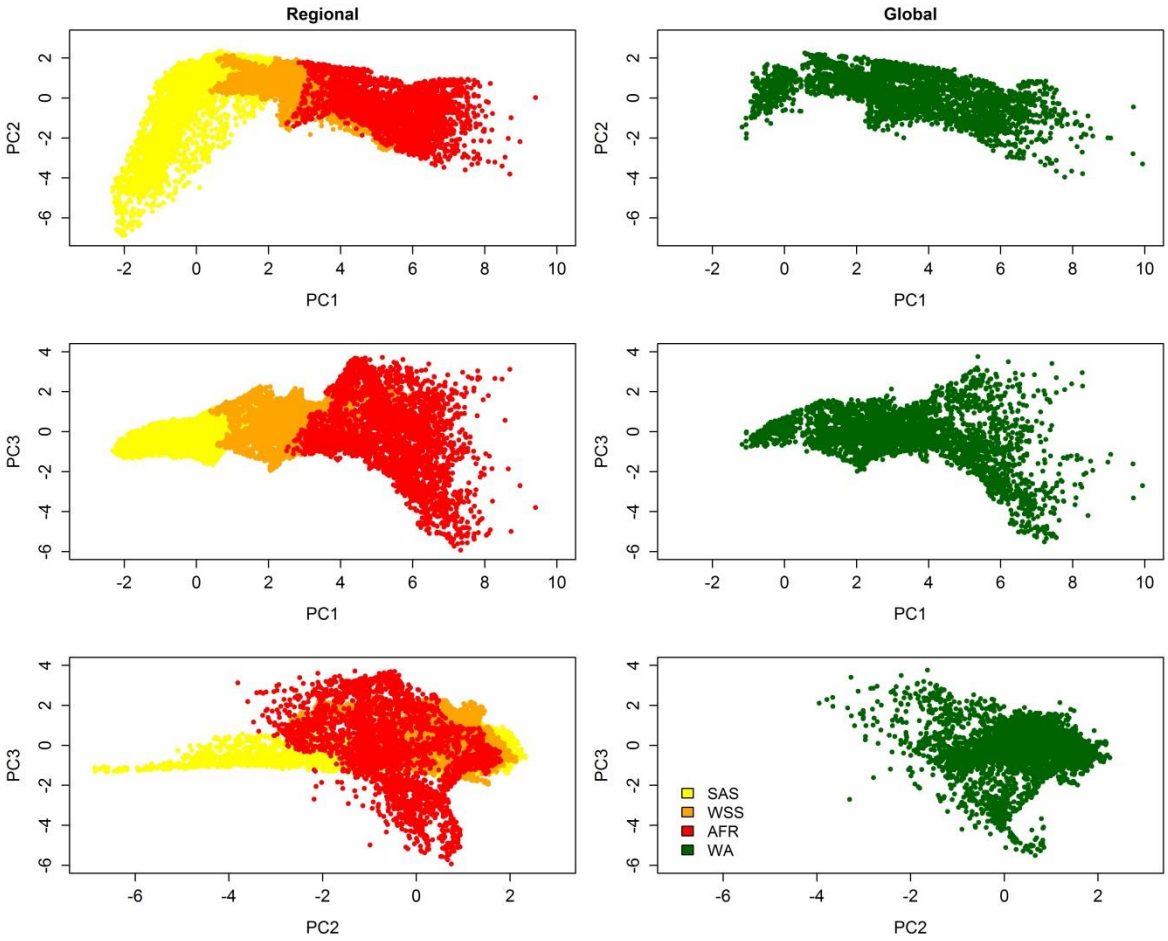

Fig. 3.11- Spatial Principal Components Analysis of the environmental variability of the study area. Environmental variability of Sahelian Acacia Savanna (SAS), West Sudanian Savanna (WSS) and Afrotropical (AFR) biogeographic areas and variability within the predicted range by the West Africa model (WA). PC1 (41.1%): distance to permanent and seasonal gueltas; PC2 (15.01%): distance to croplands and mosaic vegetation/cropland; and PC3 (17.3%): Minimum temperature of coldest month.

CONSERVATION-RELATED PARAMETERS

We based conservation-related analyses in the most accurate model, the Combined model. The identified suitable areas for Guinea baboons were restricted to the Mauritanian mountains in the Sahel, continuously distributed from Mali to Senegal and The Gambia coast in Savannah and, patchily distributed in the Afrotropical region across Guinea-Bissau, in the coastal areas between Senegal and Guinea, and in Guinea and Sierra Leone (Fig. 3.10). Approximately 21.2% of the study area was identified as suitable for the species occurrence, of which 3.9% is located in the Sahel, 70.0% in the Savannah and 26.1% in the Afrotropical regions (see Supplementary material Appendix B Table B.5). Four probable subpopulations were identified: (1) in Mauritania mountains; (2) from Mali to Senegal and The Gambia coast; (3) in Guinea-Bissau to North-east Guinea and, 4) from the region of the Outomba (between Guinea and Sierra Leone) to South-east Guinea (Fig. 3.10).

About 8.4% of predicted suitable areas are located in high human populated areas (>50 persons/km2), of which ~76.8 % were located in the Afrotropical and 23.2% in the Savannah regions (Fig. 3.10b and Appendix B Table B.5). In Mauritania, there are no suitable areas predicted in highly human populated areas. However, 19% of the predicted suitable areas are located where less than 5 people/km2are present, most of which are (~75%) in Mauritania and Mali (Fig. 3.10b). Formal protection reaches 13.3% of suitable areas, most of which are located in Savannah and Afrotropical regions. Suitable areas predicted in Sahel are not located within protected areas (Fig. 3.10b).

DISCUSSION

Our results demonstrated that models' performance depends on the spatial extent of the study area to accurately predict the current distribution of species with ecological plasticity, which has important implications to set local conservation priorities. Below, we discuss multiple aspects related to the effects of restricting the range of environmental variables and study area extent in ecological modelling of ecologically plastic species, and explore geographic differences in the environmental conditions occupied by Guinea baboons and their conservation implications.

EFFECTS OF RESTRICTING THE RANGE OF VARIABLES

We found different patterns in response curves for the predicted common variables between global (West Africa) and regional models (Sahel, Savannah and Afrotropical). Probability of species occurrence decreased abruptly as distance to permanent and seasonal gueltas increased in the Sahel model while it gradually increased after an initial decrease in the West Africa model. This result supports the opinion that restricting the range of environmental conditions over which ecological models are calibrated influenced estimations in response curves (Thuiller *et al*., 2004; Barbet-Massin *et al*., 2010). Response curves illustrated species' response to availability of suitable habitats across the range. Although some concordance was found in the importance of selected EGVs, these were not shared between all model types (see Supplementary material Appendix B Table B.3). We expected an even distribution of contributions by several EGVs in the global model, given the wide diversity of habitats occupied by the species, while contributions to the regional models would be biased towards particular variables. This expectation was well supported by the observed disproportional importance of the variable distance to permanent gueltas, which was

the most important one in the Sahel while in the global and in other regional models the importance of this variable was similar to other variables (Fig. 3.8) Such variation is probably reflecting the availability of permanent gueltas, which are only available in the Sahel, and the plasticity in the ecological niche, where distinct variables may be more important in distinct geographical areas. Still, low sample size available for testing models may also cause disagreements in the identification of the most important of variables between distinct datasets.

The Sahel model supported high regional specialization levels and a stronger connection between species presence and water availability in comparison to other regions (Brito *et al*., 2010). Such result may be related with lower availability of suitable habitats in the Sahel because the species showed much broader environmental responses in the core of the distribution (Savannah and Afrotropical regions). Ultimately, the different environmental responses observed across the range support the species ecological plasticity and highlighted the importance of particular variables at regional scales, which are probably related to local adaptations (Galat-Luong, Galat, & Hagell, 2006). As observed in our work, the use of training areas across distinct sections of the species environmental range may retrieve local niche truncation, availability of suitable habitats, and particular environmental responses (Suárez-Seone *et al*., 2014), particularly in ecological modelling of plastic species.

EFFECTS OF RESTRICTING THE SPATIAL EXTENT

The range and configuration of predicted suitable areas varied between model types. As observed before, predictions of species distribution may differ when complete or restricted species environmental range is used (Vale *et al*., 2014). Both global model and regional models adjusted to the species' occurrence, which supports the finding that ENMs perform well with extensive presence data but also within biogeographic areas (Barbet-Massin *et al*., 2010). Although the global model was able to capture the full environmental variability within species range, it tended to overestimate the species' distribution. Such overestimation was most obvious in the Savannah region where, in comparison to the regional model, the global model exhibited higher correct classification rates of the training and validation datasets but lower rate for the absence dataset, thus indicating that global model predicted high suitability in areas where the species is considered to be absent. Contrastingly, regional models tended to be more accurate, supporting previous observed differences in the performance of global and regional models to predict current distributions patterns (e.g. Suárez-Seoane *et al*., 2014; Vale *et al*., 2014). Small regions led to more accurate estimates of

species' distribution ranges (Anderson & Raza, 2010). Ecologically plastic species may occupy different suitable habitat at regional levels that could be misrepresented in global models, being encompassed by larger suitable areas. Indeed, ENMs based on the absolute environmental range may generate predictions to local unsuitable areas (Braunisch, Bollmannb, Graf, & Hirzel, 2008). For instance, suitable areas were predicted by the global model in the lower Senegal River although the region is intensively human populated and there are no evidences for the species' occurrence. In comparison with global models, regional models provided more detailed spatial distributions, allowing the definition of more accurate suitable areas where local conservation measures could be applied. For instance, both the Sahel and the Afrotropical models provide better defined suitable areas than the global model. Latter observation shows regional models can be more accurate and able to distinguish areas more suitable than others (Elith & Leathwick 2009a). Our results clearly indicate that regional models built within an ecologic significant area (e.g. biogeographic areas) should be preferred than global models for species with ecological plasticity and to set local oriented priorities for conservation.

EFFECTS OF GEOGRAPHICAL DIFFERENCES IN ENVIRONMENTAL CONDITIONS

Guinea baboons occupied distinct environmental conditions across biogeographic regions. The Sahel showed the most divergent environmental conditions. There might be a trend for niche truncation in the Sahel, as the region exhibits the most extreme arid conditions across the species range, and the species is mostly observed near gueltas (Brito *et al*., 2010). Aridity has been considered a key factor determining the level of ecophysiological stress and constraining baboon occurrence and abundance (Lara-Romero *et al*. 2012). Our results indicated little overlap in the environmental variability of each biogeographic area and also in predicted environmental conditions for Savannah and Afrotropical populations (Fig. 3.110 and Appendix B Table B.4). The gradual decline in the discordance between environmental conditions of populations in each biogeographic area supports that the species occupies distinct ecological environments along a latitudinal cline in precipitation, from arid Sahel, shrubby savannas and woodlands in Senegal and Mali to secondary forest in Guinea-Bissau (Galat-Luong *et al*., 2006; Oates *et al*., 2008; Brito *et al*., 2010).

CONSERVATION IMPLICATIONS

Predicted suitable areas followed the known distribution of Guinea baboon (Oates *et al*., 2008). The combined model identified three putative barriers to dispersal within and between regions. Isolation may be expected between: (1) Sahelian and Savannah populations, because suitable areas are spaced by ~95 km of unsuitable habitat and the highly human populated, Senegal River; (2)subpopulations restricted to Tagant-Assaba and Afollé mountains in Sahel, because these are 70 km apart and separated by the Karakoro River valley, which is mostly dry throughout the year(Campos, Sillero, & Brito, 2012) and; (3) suitable areas in North-east Guinea and Outomba in the Afrotropical region, as they are separated by ~60 km of a relatively high human density region (Fig. 4).Phylogeographic approaches using mtDNA suggested extensive and local female-biased gene flow in Guinea baboons and demonstrated weak population genetic structure and high degree of shared haplotypes among populations (Ferreira da Silva, Casanova,& Godinho, 2013; Ferreira da Silva *et al*., 2014; Kopp *et al*., 2014).Past connectivity may be related with the humid climate and savannah-like conditions at the Holocene (Kröpelin *et al*., 2008), but an increasing aridity afterwards and more recently, human activities may have contributed to population fragmentation or isolation. However, it is unknown whether contemporaneous gene-flow occurs between Sahelian and Savannah populations or between Sahelian subpopulations. Location of barriers to gene flow and genetic sub-structuring patterns in northern populations should be assessed.

The combined model suggested connectivity across Savannah and Afrotropical regions. Suitable areas in Savannah appeared to be connected to Afrotropical region along the Gambia River valley. Moreover, suitable areas in Afrotropical region tended to follow river valleys, suggesting a role as dispersal corridors. A high degree of genetic diversity found in the Boé region in Guinea-Bissau was related to the putative role of the Corubal River as a dispersal corridor (Ferreira da Silva, 2012). The Corubal River probably connects the population of Guinea highlands to the lowland populations of Guinea-Bissau. Nevertheless, these hypotheses remain untested.

Predicted suitable areas are mostly located in human-populated areas. Potential areas of conflict with human populations were identified particularly in Savannah and Afrotropical regions, where the species' range contraction was associated with extensive agricultural expansion, and targeted hunting (Oates *et al*., 2008; Ferreira da Silva *et al*., 2013). In contrast, there are no evidences of human persecution of Guinea baboon in Sahel (authors, pers. observation).

Most suitable areas currently protected are located in the Savannah region. There are no protected areas in Sahel and few in the Afrotropical region. However, protected areas are apparently crucial to the species conservation, as large groups has been observed in Niokolo-Koba National Park, in the Savannah region (Oates *et al*.,2008) and dispersing individuals in protected areas in the Afrotropical region (Ferreira da Silva *et al*., 2014). Given the high negative association between the species occurrence and human activities, a conservation programme should focus in minimizing hunting practices towards this species. Additional, suitable areas particularly with riparian galleries should be protected, given their role for the populations' connectivity foreseen by this study.

Climatic changes may threaten the northernmost populations of Guinea baboons. The association between species presence and water availability in Sahel suggests vulnerability to environmental changes. Forecasted climatic changes for Mauritanian mountains include more frequent or severe droughts (Brooks, 2004), rendering uncertain future water availability in seasonal gueltas (Brito *et al*. 2014; Vale, Pimm, & Brito, 2015). Additionally, as local communities base their economy on the exploration of the gueltas' water and the surrounding habitats, human disturbance and water pollution by livestock can become a relevant threat (Brito *et al*. 2014; Vale *et al*.2015). Management plans to minimize human impacts in gueltas should also be considered for the Mauritanian mountains.

CONCLUSIONS

Ecological modelling of species distribution may be challenging when working with ecologically plastic species. Our results show regional models calibrated in restricted environmental areas outperform models built using the complete species environmental range in accuracy. Given that ecologically plastic species may occupy different environmental areas within their range; regional models are more accurate in defining the species' environmental predictors and suitable areas. For ecologically plastic species, regional models may be the most cost-effective option for defining accurate ranges and for effectively design protected areas.

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Chapter 4

Conservation status evaluation

“Every individual matters. Every individual has a role to play.
Every individual makes a difference.”
Jane Goodall

ARTICLE III. DISTRIBUTION, SUITABLE AREAS AND CONSERVATION STATUS OF THE FELOU GUNDI (*FELOVIA VAE* LATASTE 1886)[3]

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ABSTRACT

Felovia vae is an endemic rodent from West Africa with special conservation concern. Although the global range is relatively well known, the lack of knowledge on its local distribution patterns and ecological parameters resulted in the IUCN category of Data Deficient. This study identifies environmental factors related to the occurrence of *Felovia vae*, quantifies suitable areas of occurrence, and evaluates its conservation status. High-resolution presence data (1×1 km) were combined with environmental factors to derive ecological niche-based models of species occurrence. Ecological models predicted that *Felovia vae* occurs more frequently in areas with high slope and close to gueltas, bare areas and rocky deserts. The fi ne-scaled ecological models suggest eight suitable habitat patches, representing fragmented subpopulations located in the Mauritanian mountains and in the Bafing, Felou, Nioro, and Yelimane regions of Mali. Fieldwork observations and predicted suitable areas were used to evaluate conservation status. *Felovia vae* was categorized as Least Concern, given that values for all parameters analyzed were above the thresholds of Threatened classification. The species may be susceptible to human-induced habitat loss, global warming and natural disasters, such as drought, given its reliance on water availability.

Keywords: conservation; ecological model; GIS; mountain; Red List; Sahara.

INTRODUCTION

The Felou gundi (Ctenodactylidae: *Felovia vae* Lataste 1886) is an endemic rodent from West Africa, where it is only known from the mountains of Mauritania (Adrar Atar, Tagant, Assaba and Afollé) and scattered localities in Mali, along the Senegal River valley (Dekeyser and Villiers 1956, George 1974, Le Berre 1990, Aulagnier 2008a, Padial and Tellería 2009). Recently, 40 new observations of *F. vae* were reported in Mauritanian mountains (Brito *et al*. 2010), providing further evidence for the mountain-restricted character of the species. *Felovia vae* has been reported to be a rock outcrop specialist (George 1974), and in Mauritania it was observed in river canyons, particularly in the proximity of rock pools (locally known as guelta), boulder grounds, and cliffs (Padial and Tellería 2009, Brito *et al*. 2010).

Although the global range of *Felovia vae* is relatively well known, there are many knowledge gaps concerning local distribution and fragmentation levels in West Africa. For instance, populations from Mauritania and Mali are apparently isolated (Brito *et al*. 2010). Thus, high accuracy mapping of suitable areas for species occurrence and the evaluation of potential connectivity between populations of southern Mauritanian mountains with populations in Mali should be considered priority for the development of optimized local conservation strategies. Also, it has been suggested that populations within Mauritanian mountains may be fragmented by probable unsuitable habitats, such as permanently dry and dune-covered areas (Brito *et al*. 2010). Nevertheless, the contribution of climatic and habitat factors to the isolation of this species remain unknown.

Felovia vae has been considered threatened by deforestation and desertification (Schlitter 1989, Amori and Gippoliti 2003) and an African rodent of special conservation concern (Schlitter 1989). Probably there has been a decrease in habitat quality as a consequence of the severe droughts that affected the Sahel region from the 1970s onwards (Ahmed *et al*. 2008, Mahé and Paturel 2009), inducing local extinction in other vertebrates (Trape 2009). In addition, changes in availability of suitable habitats may also occur in the future as a result of the forecasted climatic changes for the region (Brooks 2004, Held *et al*. 2005). Nevertheless, the lack of knowledge on population size, range dimensions, ecology and population trends of the species resulted in the IUCN category of Data Deficient (DD) (Aulagnier 2008a).

The aims of this study are to identify environmental factors related to the occurrence of *Felovia vae*, quantify suitable areas for species occurrence, and evaluate its conservation status. High-resolution presence data (1×1 km) will be combined with

environmental factors to derive ecological niche based models of species occurrence. Fieldwork observations and predicted suitable areas will be used to evaluate conservation status.

MATERIALS AND METHODS

The study area is located in West Africa, between 12.5°N and 23.5°N, and west of 5.0°W, covering Mauritania, southern Morocco, Senegal, The Gambia and south-western Mali (Fig. 4.1). In Mauritania, there are four main mountain massifs: the Adrar Atar in the central region, and the Tagant, Assaba and Afollé in the southern regions of the country. The Adrar Atar is separated from the remaining mountains by the El Khatt river basin, whereas the Tagant-Assaba Mountains are separated from the Afollé by the Karakoro river basin (Fig. 4.1). The two river basins lack significant rock outcrops and they are dune-covered, but whereas the El Khatt is permanently dry, the Karakoro is subjected to seasonal run-offs and it is relatively populated. Most of the study area is covered by sandy, stony and bare deserts (30.0%, 17.9%, 10.0%, respectively; Bicheron *et al.* 2008), but croplands and mosaics cropland- vegetation (17.6%), and closed to open shrublands and grasslands (11.8%) are more frequent in southern regions.

A total of 61 observations (localities) were used to develop models (Dekeyser and Villiers 1956, George 1974, Nickel 2003, GBIF 2009, Granjon and Duplantier 2009, Padial and Tellería 2009, Brito *et al*. 2010) (Fig. 3.1). Observations were collected from the period between 1956 and 2010, although 90% are post-2000. For 46 observations, the geographic location was recorded with a Global Positioning System (GPS) on the WGS84 datum (Brito *et al*. 2010), whereas the remaining 15 bibliographic observations included localities with geographic coordinates or with clear toponomies from which it was possible to gather coordinates from topographical maps (Institut Géographique National, IGN) to a precision of 1 km. The number of individuals was quantified by direct observation in 40 localities of Mauritania. Quantifications were made while sampling for other taxonomic groups (see Brito *et al*. 2010 for details). No traps were set or direct search of pellets was performed, which could have increased the total number of individuals detected.

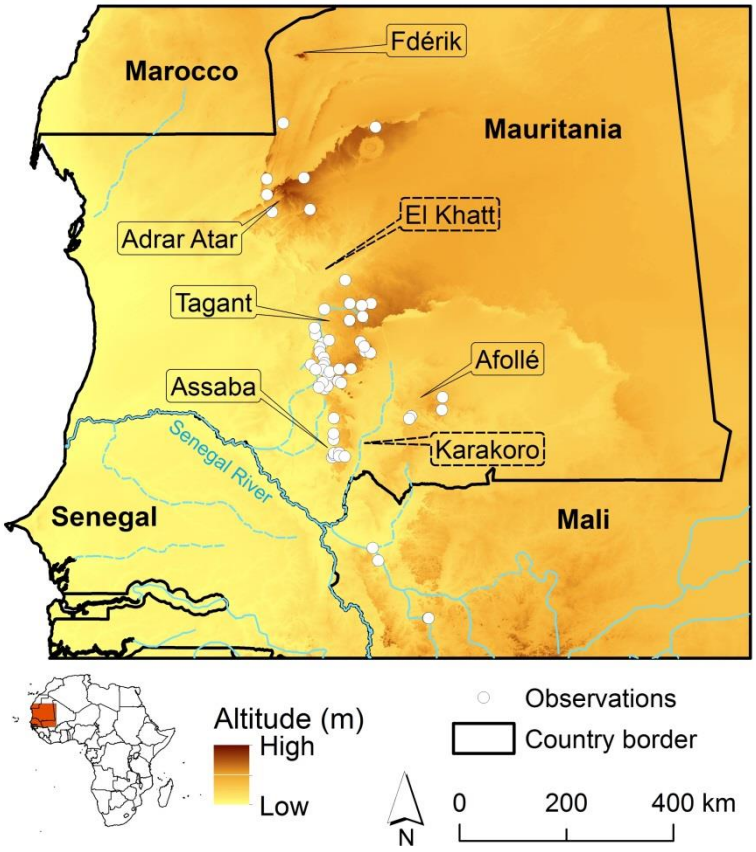

Fig. 4.1- Distribution of observations of *Felovia vae*, major toponomies in the study area, and location of the study area in the African context. River names are given in stippled boxes.

Given that survey effort in Mauritania was spatially biased (mountains were more heavily sampled), resulting in observation clumps, it was necessary to reduce the level of spatial autocorrelation to avoid potential biases in model predictions (Phillips *et al*. 2009). From the global data set (n=61), observations were removed from clusters of species occurrence, resulting in two data sets: one with 28 observations for training and testing models and another one with 33 observations that was used to calculate the extent of occurrence (see below). The Nearest Neighbour Index was used to assess the degree of data clustering (Brito *et al*. 2009): 0.60 in the global data set (n=61) and 1.14 in the data set for model building (n=28), indicating dispersed distribution for the latter. Spatial analyses were done with “Spatial Analyst” extension of ArcGIS 9.2 (ESRI 2006).

Ecogeographical variables (hereafter EGVs) were selected for the ecological models according to their relationship with the ecology and distribution of *Felovia vae* (George 1974, Padial and Tellería 2009, Brito *et al*. 2010). EGVs included: (i) one topographical grid (USGS 2006) that was used to derive Slope, with the “Slope” function of ArcGIS; (ii) six climate grids (Hijmans *et al*. 2005); (iii) a land cover grid from the years 2004 to 2006 (Bicheron *et al*. 2008); and (iv) the presence of gueltas, digitized from the IGN

maps for the all study area, and ground-validated by fieldwork only in Mauritania (Table 4.1). To convert the categorical land cover and presence of gueltas EGVs into continuous variables, one binary grid was created for each habitat type that covered more than 5 % of the study area and for the presence of gueltas. The Euclidean distance of each grid cell to the closest habitat type was calculated for each individual habitat grid (nine habitat types) using the "Euclidian Distance" tool of ArcGIS (Brito *et al*. 2009). The same procedure was applied to presence of gueltas. A total of 10 "distance to" EGVs were analyzed (Table 4.1). Finally, the resolution of all EGVs was decreased to a grid cell size of 0.0096 degrees (1 × 1 km) by averaging the EGV values inside each grid cell.

Table 4.1. Environmental factors used for model the distribution of *Felovia vae* in the study area

Type	Variable	Range and units
Topographical	Slope	0 - above 26%
Climatic	Annual mean temperature	20.4 - 30.8ºC
	Maximum temperature of warmest month	27.1 - 48.0ºC
	Minimum temperature of coldest month	8.5 - 18.9ºC
	Temperature annual range	14.0 - 39.3ºC
	Annual Precipitation	11 - 1334mm
	Precipitation of wettest month	4 - 455mm
Habitat	Distance to croplands	0 - 7.51°
	Distance to mosaic cropland / vegetation	0 - 7.62°
	Distance to mosaic vegetation / cropland	0 - 6.99°
	Distance to closed to open shrubland	0 - 7.63°
	Distance to closed to open herbaceous vegetation	0 - 6.02°
	Distance to sparse vegetation	0 - 6.05°
	Distance to bare areas	0 - 1.34°
	Distance to consolidated bare areas (rocky desert)	0 - 3.73°
	Distance to non-consolidated bare areas (sandy desert)	0 - 4.92°
	Distance to gueltas	0 - 8.17°

Ecological niche-based models were developed with the Maximum Entropy approach (Phillips *et al*. 2006). Model input variables included slope, six climatic variables and 10 distances to habitat type EGVs. A total of 10 model replicates were run with random seed. Observations for each replicate were chosen by bootstrap allowing sampling with replacement in each model replicate. Observations were randomly chosen as test data (10 %) for each model. Models were run with auto features and logistic output (Phillips *et al*. 2006). The area under the curve (AUC) of the receiver-operating characteristics (ROC) plot was taken as a measure of model fitness (Fielding and Bell 1997). The 10 replicates were averaged to generate a forecast of species presence probability (average model), which is a robust procedure to derive consensus predictions of species likelihood of presence (Marmion *et al*. 2009). Given that predictions can fluctuate between individual models, the standard deviation (SD) of model replicates was used as an indication of prediction reliability (Buisson *et al*. 2010, Carvalho *et al*. 2010).

The importance of each EGV for explaining the distribution of the species was determined by its average percent contribution to the models. The relationship between species occurrence and EGVs was determined by the visual examination of response curves profiles from univariate models (Brito *et al*. 2009).

To quantify suitable areas for species presence, the average model was reclassified to display grid cells of probable absence and presence. The threshold of minimum probability for species presence (p=0.0263) was chosen in order that all observations (n=61) occurred in grid cells of probable presence (suitability model).

The evaluation of the conservation status followed the methodology and criteria of IUCN Guidelines for Red Lists (IUCN Standards and Petitions Working Group 2014). Criteria of population reduction (A), geographic range (B), small population size and decline (C), and very small or restricted population (D) (IUCN Standards and Petitions Working Group 2014) were applied using Ramas Red List software (Akçakaya and Ferson 2001). Parameters for classification included: (i) population number, estimated from the number of mature individuals found during field sampling, the number of locations where the species was observed (see below, iv), and the area of occupancy predicted for the species by the suitability model (see below, iii); (ii) extent of occurrence, estimated by a minimum convex polygon method, which determines the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all observations (n=61) and the suitable area predicted by modelling. Calculations were made using Hawth' s Tools extension for ArcGIS (Beyer 2006); (iii) area of occupancy, calculated from the number of suitable cells predicted by the

suitability model × area of a grid cell (1×1km2); and (iv) population fragmentation, evaluated based on the number of subpopulations, which were quantified by the number of isolated suitable patches predicted by the suitability model, and the number of locations, quantified from the number of uncorrelated observations (training data set). Population reduction and continuous decline estimates were inputted in Ramas with values below the thresholds for Threatened taxa classification (30% of reduction and 10–25% of continuous decline, according to future time periods).

RESULTS

The ROC plots exhibited high average AUCs for both training and test data sets: 0.994 (±0.008 SD) and 0.985 (±0.012 SD), respectively. Average highest SD of individual models occurred mostly in mountain tops (Fig. 4.2). The ecological models identified distance to gueltas as the EGV most contributing to the individual models (average 63.9 ±10.70% SD), followed by slope (18.0 ±8.24%), distance to bare areas (5.64 ±4.7%), and rocky deserts (2.21 ±2.00 %). All other EGVs had average contributions lower than 2 %. The average profiles of response curves for these EGVs suggested that the species occurs more frequently in areas with high slope and close to gueltas, to bare areas, and to rocky deserts (Fig. 4.3).

The average model identified areas for the occurrence of *Felovia vae* in almost all Mauritanian mountain regions and also southwestern Mali (Fig. 4.2). The El Khatt and Karakoro river valleys were identified as unsuitable for species occurrence. The suitability model identified approximately 6.8 % of the study area as suitable for the occurrence of F. vae, of which 89.8 % of suitable cells were located in the mountains and escarpments of Mauritania (81,946km^2), 8.1 % in localized areas in Mali (7415km^2), and 2.1 % in scattered grid cells in Senegal, and Morocco (Fig. 4.2).

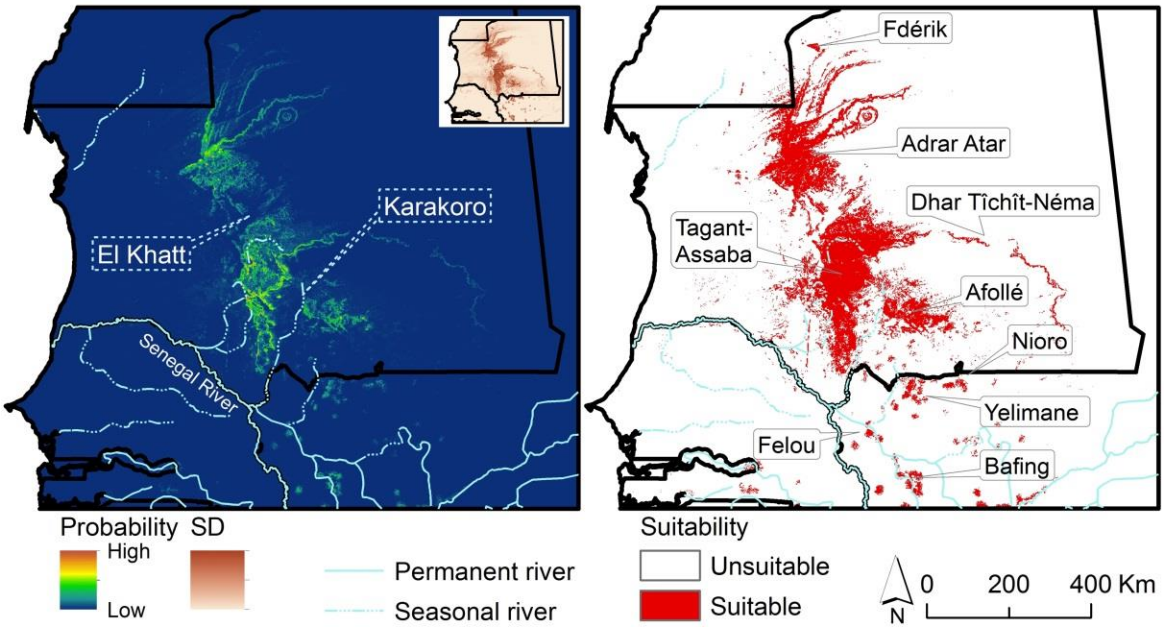

Fig. 4.2- Average probability of occurrence of *Felovia vae* and standard deviation (small inset at left) estimated by the ensemble of 10 Maximum Entropy models (left). Predicted suitability areas and subpopulations considered for evaluation of the conservation status (right).

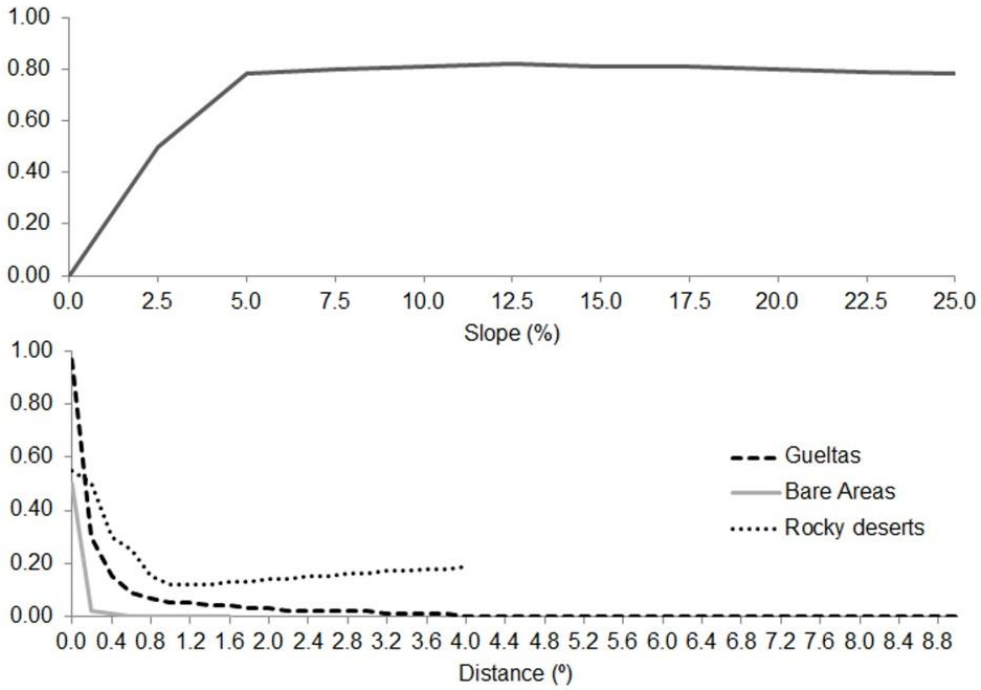

Fig. 4.3- Response curves for the environmental factors most related to the occurrence of *Felovia vae* in the study area.

The extent of occurrence and area of occupancy were estimated to be 263,035 km 2 and 80,003 km 2, respectively, and eight fragmented subpopulations were identified: Fdérik, Adrar Atar, Tagant-Assaba and Afollé in Mauritania, and Bafing, Felou, Nioro, and Yelimane, in Mali (Fig. 4.2). Although the total number of locations is unknown, it should be much higher than 10 (threshold for Threatened classification), given the number of uncorrelated observations (n=28) of *Felovia vae* detected. The number of individuals in each group observed during the fieldwork in Mauritania ranged from one to around 25 (average 8.4 ±5.4 SD) in each of the 40 localities sampled. Most groups included five (32.5%) or 10 individuals (40%), whereas larger groups of 25 individuals and smaller groups with fewer than three individuals were less common (12.5% and 15%, respectively). Taking into account the area of occupancy and the average number of individuals detected in each locality, the total number of mature individuals is probably much higher than 10,000 individuals (threshold for Threatened classification).The input of these parameters in Ramas software gave the conservation status of Least Concern (LC).

DISCUSSION

The ecological models combined topographical, climatic and habitat variables to understand probable relationships between *Felovia vae* occurrence and environmental gradients. Results suggest that species occurrence is mostly related to topography and land cover and not climatic variability. *Felovia vae* was thought to occur in river canyon walls, rocky outcrops, cliffs, boulder slopes, and treeless habitats (George 1978, 1979, de Rouffignac *et al*. 1981, Padial and Tellería 2009, Brito *et al*. 2010), where in fact, probability of presence increased with slope and proximity to bare areas, rocky deserts, and gueltas, which are mostly associated with mountains. Distance to gueltas was the most important environmental factor related to species presence and it is probably associated with the presence of rock outcrops and water availability. Although gundis have been reported to rely on vegetation to regulate their water intake (de Rouffignac *et al*. 1981), *F. vae* was observed drinking water from gueltas in southern Assaba mountains (Fig. 4.4). In the mountains of Mauritania, gueltas may be the only water source available for large distances (C.G. Vale *et al*., personal observation).

Areas of probable occurrence identified for West Africa follow the general distribution patterns previously identified for the species (George 1974, Padial and Tellería 2009, Brito *et al*. 2010). Nevertheless, the fine-scaled ecological models allowed the definition of accurate suitable habitats. For instance, an observation of *Felovia vae* in

Kediet Idjil (Fdérik) from the 1940s (Le Berre 1990), which was considered dubious and not used in model training or testing, was identified as a suitable area. The predicted suitable areas from where the species is presently unknown should be sampled in the future, particularly the Malian regions of Nioro and Yelimane, and the Mauritanian escarpments of Dhar Tîchît-Néma.

Fig. 4.4- *Felovia vae* drinking water from a guelta in southern Assaba mountain (December 2007). Photograph by A.L. Acosta.

The models suggest that suitable areas are restricted mostly to isolated mountain habitats. For instance, suitable areas in the Adrar Atar are separated from the Tagant-Assaba by at least 20km of unsuitable habitat, in the region of the dry and dune-covered El Khatt river basin, and suitable areas in the Tagant-Assaba are separated from the Afollé by at least 25km, along the Karakoro river basin. Relatively large distances between suitable patches in southern Mauritania and Mali are around 130km apart from Felou. Additionally, the lower Senegal River is predicted as unsuitable, further supporting the likely isolation of Mauritanian populations. Probably, the isolation of Mauritanian subpopulations increased progressively after the mid-Holocene, with the gradual drying of the savannah-like ecosystem and development of arid conditions (Kröpelin *et al*. 2008). Although the ranging behavior of *F. vae* is unknown, its relatively small body size and habitat specialization may hamper dispersal and the gene flow between the eight potential subpopulations identified. Nevertheless, studies with

molecular markers are needed to determine if genetic sub structuring occurs among distinct subpopulations of this mammal.

The number of individuals observed in each group was larger compared to previous estimations for Mauritania (Padial and Tellería 2009). Although the present study lacked specific methodology for population estimation, similar group sizes were reported in Mauritania (Padial and Tellería 2009) as in Felou (up to 25 individuals; George 1974).

Felovia vae was categorized as Least Concern, given that all parameters analyzed exceeded the thresholds for categorization as Threatened. However, threats to the species include human-induced habitat loss, global warming and natural disasters, such as drought (Schlitter 1989, Amori and Gippoliti 2003, Padial and Tellería 2009). Given the close relationship with water availability, population size is likely to have declined because of droughts in the 1970s (Ahmed *et al*. 2008, Mahé and Paturel 2009). The species may also be negatively affected by climate changes, as climate models predict more frequent or severe droughts for the region (Brooks 2004, Held *et al*. 2005). Thus, although a decrease of habitat quality may be suspected for both past and future (18 years range) periods, population reduction and continuous decline estimates were inputted in Ramas with values below the thresholds for Threatened taxa classification. Quantitative data on population size and trends are needed to better estimate population reduction parameters and assess species vulnerability to climate change.

The suitable areas predicted for *Felovia vae* are mostly restricted to Mauritanian mountains. Their biological value is being increasingly quantified (Tellería *et al*. 2008, Padial and Tellería 2009, Trape 2009, Brito *et al*. 2010, Padial *et al*. in press) and these results also highlight the importance of these island-like mountains. Although, recently the Lake Gabbou and the Hydrological Reserve of Tagant Plateau were designated as Ramsar site (Ramsar 2009), these results further suggest that the establishment of protected areas should be considered for the remaining mountains to minimize human induced threats.

Distribution and habitat selection patterns observed in this study may give indications about other desert gundis with fragmented distributions and similar habitat requirements, such as *Massoutiera mzabi*. This species is usually found on the slopes of mountains and river banks, living in rocky fissures where water accumulates after the rains and relatively rich vegetation develops (George 1981, Gouat *et al*. 1984, Aulagnier 2008b). Although the relationship of *M. mzabi* with water availability is unclear, the species apparently presents morphological adaptations to dry conditions (Gouat 1993). Therefore, the methodological approach used here should be applied to

other desert isolated species, particularly to other gundis, for the quantification of suitable habitats.

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ARTICLE IV. DISTRIBUTION, SUITABLE AREAS AND CONSERVATION STATUS OF THE BOULENGER'S AGAMA (*AGAMA BOULENGERI*, LATASTE 1886)[4]

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ABSTRACT

Agama boulengeri is a West African endemic lizard. It occurs in arid rocky areas in the Mauritanian mountains and Kayes region of Mali. Data on the distribution of *Agama boulengeri* is however very coarse, and the contribution of climatic and habitat factors for population isolation are unknown. Using Maxent, GLM, and high resolution data, we generated environmental niche models, and quantified suitable areas for species occurrence. Field observations and predicted suitable areas were used to evaluate the conservation status of *Agama boulengeri*. Results revealed the species occurs preferentially close to gueltas, bare areas, and rocky deserts and in areas of increasing rainfall. Suitable cells were mostly located in Mauritania, and four potentially fragmented subpopulations were identified. The conservation status of *Agama boulengeri* was determined to be of Least Concern.

Keywords: Ecological Niche Models; Endemic; IUCN status; Mauritania; West Africa

INTRODUCTION

The Boulenger's agama (*Agama boulengeri* Lataste 1886) is a Sahelo-Saharan agamid, endemic to West Africa. The species is restricted to Mauritanian mountains (Adrar Atar, Tagant, Assaba and Afollé; Padial, 2006) and a few localities of the Kayes region in Mali (Joger and Lambert, 1996). *Agama boulengeri* has been associated with very arid rocky areas lacking vegetation cover (Geniez *et al*., 2004), being observed in rocky walls (de La Riva and Padial, 2008), but the species probably occupies more productive environments in the extreme southern range. To date, studies are lacking on local distribution and fragmentation levels, which results in a lack of knowledge regarding range size, and population size and number. A recent work about genetic variation of North African agamas reported two clusters of *A. boulengeri* restricted to northern and southern mountains of Mauritania (Gonçalves *et al*., 2012). Reproductive isolation between populations may be related to unsuitable habitats, such as permanently dune-covered areas separating Mauritanian mountains. Nevertheless, the contribution of climatic and habitat factors for population isolation remains unknown and high accuracy mapping of suitable areas for species occurrence should be considered a priority for the development of optimized local conservation strategies. *Agama boulengeri* was proposed to be included in the Lower Risk – Near Threatened (LR-NT) category of the IUCN red list (Geniez *et al*., 2004), but the species remains unlisted, probably due to the lack of knowledge about its biology, ecology, distribution and population trends.

The aims of this study were to identify environmental factors related to the occurrence of *A. boulengeri*, quantify suitable areas for species occurrence, and evaluate its conservation status. We combined high-resolution presence data (1x1km) with environmental factors to derive ecological niche-based models of species occurrence. Field observations and predicted suitable areas were used to evaluate conservation status.

METHODS

The study area was located in West Africa between 12.5ºN and 23.5ºN, and west of 5.0ºW, covering Mauritania, southern Morocco, Senegal, The Gambia, and south-western Mali (Fig. 4.5). In Mauritania, there are four main mountain massifs: the Adrar Atar in the central region, and the Tagant, Assaba and Afollé in the southern regions of the country. The Adrar Atar is separated from the remaining mountains by the El Khatt

river basin, while the Tagant-Assaba mountains are separated from the Afollé by the Karakoro river basin. The two river basins lack significant rock outcrops and they are dune-covered, but while the El Khatt is permanently dry, the Karakoro is subjected to seasonal run-offs. Most of the study area is covered by sandy, stony and bare deserts (30.0%, 17.9%, 10.0%, respectively; Bicheron *et al*., 2008). Cropland and cropland-vegetation mosaics (17.6%), and closed to open shrubland and grassland (11.8%), are present in the southern region.

A total of 166 observations (localities) of *A. boulengeri* were used to develop ecological niche-based models (Fig. 4.5). From these, 147 observations were collected during 10 fieldwork missions to Mauritania (http://cibio.up.pt/crocodilos/en/missions) that sampled 813 localities (Brito, 2003; authors' unpublished data). The geographic locations of fieldwork observations were recorded using a Global Positioning System (GPS). The remaining 19 bibliographic observations included georeferenced localities or clear toponomies from which coordinates were collected (Institut Géographique National, IGN) to a precision of 1 km (Dekeyser and Villiers, 1956; Valverde, 1957; Joger, 1979; Le Berre, 1989; Joger and Lambert, 1996; Pleguezuelos *et al*., 2004; Geniez *et al*., 2004; Geniez and Arnold 2006; Padial 2005, 2006). From the initial dataset of observations, data were selected to develop ecological niche-models from clusters of species occurrence. Therefore, models were built using a dataset of 94 non-spatially aggregated observations (the minimum distance between observations was 10km), according to the Nearest Neighbour Index of ArcGIS 10.0 (ESRI, 2011). The remaining 72 observations were used for model validation and to calculate the threshold for species presence and the extent of occurrence (see below). Two datasets of pseudo-absences were built: a random dataset of pseudo-absences (RAbs; N=2000) and an absence dataset informed by fieldwork (FAbs; N=94). FAbs dataset was randomly created and then corrected by fieldwork information, to insure that all absences were located in areas where the species was not detected. Both datasets were created within a buffer of 100 km around the presence dataset and distant from the presence data by at least 20km.

Ecogeographical variables (hereafter EGV) included: 1) one topographical grid (USGS, 2006) that was used to derive Slope, with the "Slope" function of ArcGIS; 2) three climate grids (Hijmans *et al*., 2005); 3) four distance to habitats grids derived from a land-cover grid for the years 2004-2006 (Bicheron *et al*., 2008); and 4) distance to rock pools (locally known as gueltas), digitised from the IGN maps, and ground-validated in Mauritania by fieldwork (Table 4.2). For converting categorical land cover and presence of gueltas EGVs into continuous variables, one binary grid was created for each habitat type that covered more than 5% of the study area and for the presence of

gueltas. The distance to variable layers were processed using Euclidean distance of each grid cell to the closest habitat-type cell (Brito *et al*., 2009) using the "Euclidean Distance" tool of ArcGIS. All EGVs were used at the original square pixel size of 30" (~1km). Correlation coefficients indicated low correlation (r<0.73) between EGVs, with the exception of distance to rock and precipitation (r = 0.86).

Table 4.2 - Environmental variables used for modelling the distribution of *Agama boulengeri*. Percentage of contribution (%cont) derived from maximum entropy models. The coefficient (β) and the maximum (Max), minimum (Min), average (Avg) and standard deviation (SD), and significance (signif.) of each variable for generalized linear models (GLM) derived with random pseudo-absences (RAbs) are given. The coefficient (β), standard error (SE) and significance (signif.) of each variable for GLM model derived absences supervised by fieldwork (FAbs) are given. Significance codes are: '***' p<0.001; '**' p<0.01; '*' p<0.05.

EGVs description	West Africa	GLM RAbs				GLM Fabs		
	% Cont	Max (β)	Min (β)	Avg β (SD)	Signif	β	SE	Signif
Annual precipitation	0.62	0.03	0.01	0.02 (0.00)	***	0.02	0.02	***
Maximum temperature of warmest month	0.20	0.14	-0.04	0.04 (0.05)		0.14	0.06	
Annual average potential evapotranspiration	0.26	0.00	-0.02	-0.01 (0.01)		-0.02	0.01	
Distance to mosaic cropland /vegetation	1.08	1.36	0.53	0.94 (0.23)		0.96	0.40	**
Distance to bare areas	4.21	24.00	12.51	17.98 (3.33)	***	-19.83	6.92	***
Distance to consolidated bare areas (rocky deserts)	1.47	0.38	-6.08	-3.86 (1.63)		-4.55	1.83	
Distance to seasonal rivers	0.96	0.11	-1.28	-0.62 (0.40)		-1.14	0.49	*
Distance to *gueltas*	90.12	-2.69	-4.81	-3.59 (0.49)	***	-3.48	0.82	***
Slope	1.07	1.56	0.15	0.61 (0.33)		0.91	0.33	***

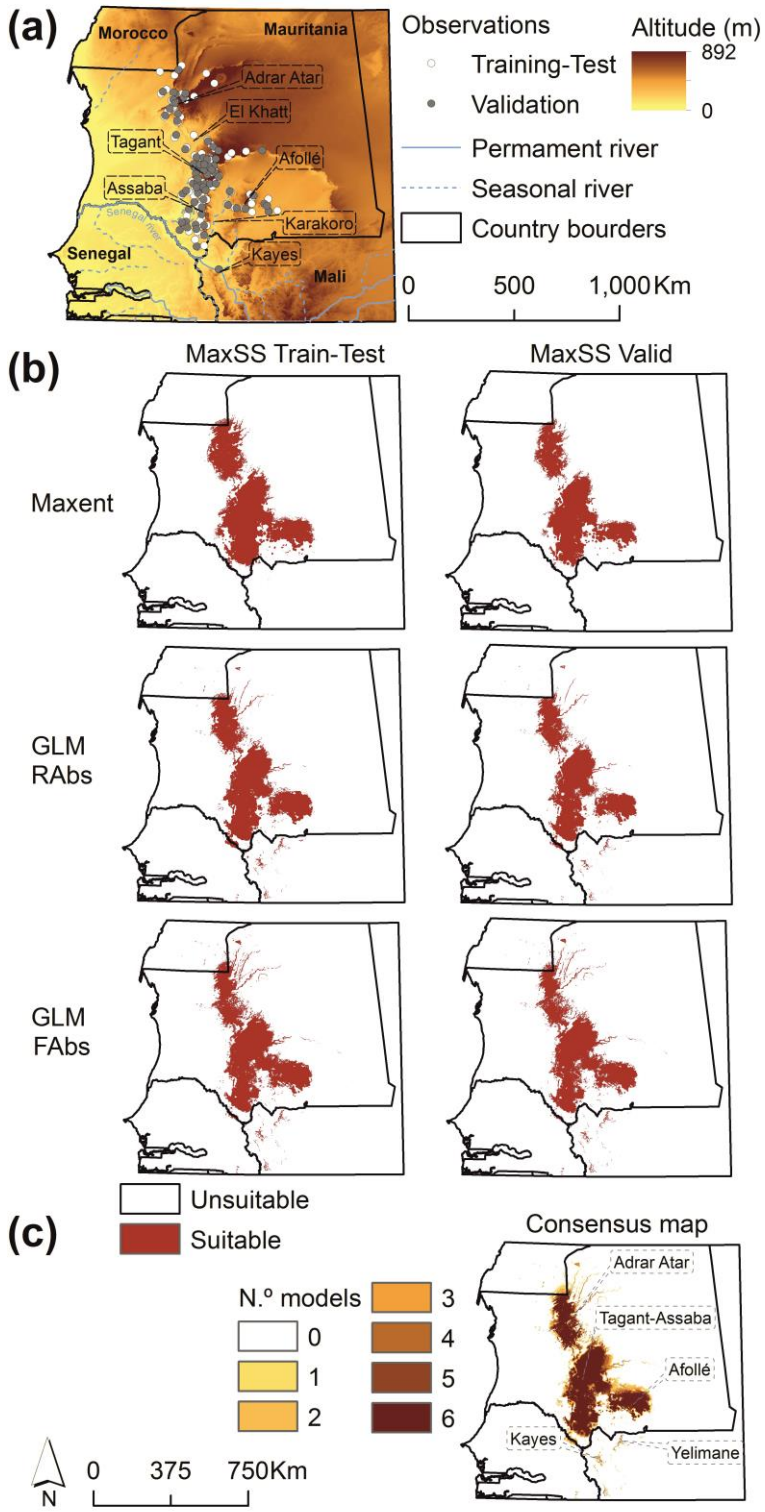

Fig. 4.5 - Distribution of *Agama boulengeri* observations (a). Binary predictions of species presence according to maximum entropy and generalized linear models (GLMs) and according to two thresholds: maximum sensitivity plus specificity threshold calculated with the training and validation datasets (MaxSS Train-Test and MaxSS Valid, respectively). GLM models were derived with random pseudo-absences (RAbs) and absences supervised by fieldwork (FAbs) (b). Consensus prediction (six out of six models) was derived from the ensemble of binary predictions (c). This figure is published in color in the online version.

Ecological niche-based models were developed using the Maximum Entropy approach, implemented in Maxent 3.3.3 beta software (Phillips *et al*., 2006), and the generalized linear model (GLM; McCullagh and Nelder, 1989). A total of 20 Maxent model replicates were built with 20% of test data (19 observations) chosen by bootstrap with random seed, auto-features, and logistic output (Phillips *et al*., 2006). Area under the curve (AUC) of the receiver-operating characteristics (ROC) plot was taken as a measure of model fitness (Fielding and Bell, 1997). The 20 replicates were averaged to generate a forecast of species presence probability, which is a robust procedure to derive consensus predictions of species likelihood of presence (Marmion *et al*., 2009). Percentage of contribution of EGVs to the models was used to identify variables most related to species occurrence (Brito *et al*., 2009, 2011). Twenty replicate GLM models were built using the RAbs dataset and one GLM model with the FAbs datasets. An ANOVA was performed to determine the importance of EGVs for explaining species distribution and their significance for each model (chi-squared test) and coefficients were checked to identify relationships between species occurrence and environmental variation. The analysis was done in R software v. 2.13 (R Development Core Team, 2011).

Probability models (Maxent, GLM RAbs and GLM FAbs) were reclassified to display grid cells of probable absence and presence. The maximum training sensitivity plus specificity threshold (MaxSS) was used since it minimises both omission and commission errors (Liu *et al*., 2005). The best cut-off value corresponds to the point on the ROC curve where sensitivity and specificity are maximised, i.e. where the total amount of misclassification is minimised (Braunisch and Suchant, 2010). Max SS thresholds were calculated for both training and validation datasets (MaxSS Train and MaxSS Valid, respectively) resulting in a total of six models. The six binary models were added to derive an ensemble prediction of probable presence and absence. Consensus predictions were validated by calculating correct classification rates of both presence and absence data.

The conservation status assessment followed the methodology and criteria of IUCN guidelines for red lists (IUCN SPWG, 2008). Criteria of population reduction, geographic range, small population size and decline, and very small or restricted population (IUCN SPWG 2008) were applied using Ramas Red List software (Akçakaya and Ferson, 2001). These criteria were estimated using: 1) population number, from the number of mature individuals found during field sampling, the number of locations where the species was observed (see below 4), and the area of occupancy predicted for the species by models (see below 3); 2) extent of occurrence, by a minimum convex polygon method, which determines the area contained within the

shortest continuous boundary which can be drawn to encompass all observations (N=166) and the suitable area predicted by modelling (Vale, Álvares and Brito, 2012); 3) area of occupancy, from the number of suitable cells predicted by six models in the consensus map × area of a grid cell (1x1 Km2); and 4) population fragmentation, evaluated based on the number of subpopulations, which were quantified by the number of isolated suitable patches forecasted by consensus predictions, and the number of locations, quantified from the number of unclustered observations (training dataset). Population reduction and continuous decline estimates were input into Ramas with values below the thresholds for Threatened taxa classification (30% of reduction and 10 to 25% of continuous decline, according to future time periods).

RESULTS

The Maxent ROC plots exhibited high average AUCs for both training and test datasets: 0.97 (± 0.01 sd) and 0.96 (± 0.01 sd), respectively. Maxent and GLM models identified distance to gueltas as the most important EGVs related to the distribution of *A. boulengeri*, followed by distance to bare areas (Table 4.2). Distance to rocky deserts and annual precipitation were also relevant according to Maxent and GLMs, respectively. The coefficients (β) of these EGVs on GLM models suggested positive relationships between species presence with increasing annual precipitation and negative relationships with increasing distances to gueltas and to rocky deserts (Table 4.2).

The correct classification rate of presences and absences according to the consensus prediction were 93.4% and 81.9%, respectively. Predicted suitable areas for *A. boulengeri* were consistent between model types and thresholds (MaxSS Train and MaxSS Valid, Fig. 4.5). Consensus predictions were mostly restricted to Mauritanian mountains, while four individual models also predicted presence in south-western Mali. Consensus predictions identified about 5.3% of the study area as suitable for the occurrence of *A. boulengeri*, of which 99.8% of suitable cells were located in the mountains and escarpments of Mauritania (84,514km2), 0.1% in scattered grid cells in Senegal (~85 km2), 0.07% in localized areas in Mali (~58km2) and 0.03% in Morocco (~24km2).

The extent of occurrence and area of occupancy were estimated to be 291,741 km2 and 84,664 km2 respectively, and four potentially fragmented subpopulations were identified: Adrar Atar, Tagant-Assaba and Afollé in Mauritania, and Kayes at Mali (Fig. 4.5). Taking into account the number of un-clustered localities (N=94) and the number

of different locations (~281) where *Agama boulengeri* was observed, they clearly exceed the threshold for Threatened classification (10 localities). The total number of mature individuals should be also much higher than 10,000 individuals (threshold for Threatened classification), given the area of occupancy and the count number of localities where the species was observed and the detectability of the species during the fieldwork. The input of these parameters in Ramas software gave the conservation status of Least Concern (LC).

DISCUSSION

Ecological models allowed understanding of probable relationships between *Agama boulengeri* occurrence and environmental gradients. Results suggested that presence probability of the species increases near gueltas, bare areas and rocky deserts, and with annual precipitation. Indeed, the species has been associated with arid rocky areas lacking vegetation and to wet rocky gorges (gueltas) in the mountain areas (Geniez *et al*., 2004; Padial, 2005). All model types identified distance to gueltas as the most important environmental variable related to species presence and it is probably associated with the presence of rock walls, where the species has been observed (de La Riva and Padial, 2008).

Predicted suitable areas followed the expected distribution pattern for the species (Joger and Lambert, 1996; Geniez *et al*., 2004; Padial, 2006). Yet, the combination of fine-scale ecological models and two model techniques allowed the definitions of accurate suitable areas for species presence. For instance, Yelimane at Mali was predicted to be suitable for occurrence, but there are no records of species presence. Future sampling is needed to assess the species' presence in the region.

The suitable areas of *A. boulengeri* predicted by consensus between six models are mostly restricted to isolated mountain areas. Relatively small distances between patches of suitable areas were predicted by the consensus. Suitable areas in the Adrar Atar are separated from the Tagant-Assaba, in the narrowest fringe, by 5 km of unsuitable habitat, in the region of the dry and dune-covered El Khatt river basin. Yet, suitable areas in the Tagant-Assaba are separated from the Afollé by at least 3 km, along the Karakoro river basin, which lacks rock outcrops. On the other hand, relatively large distances between suitable patches in southern Mauritanian mountains and Mali were forecasted by the consensus of the six models. Suitable areas in southern Assaba were predicted to be separated from Kayes by a 60 km wide-band corresponding to the unsuitable lower Senegal river which supports the likely isolation

of Malian populations. Although *A. boulengeri* home range and dispersal capability are unknown, its relatively small body size (total length ~30cm) and habitat specialization may hamper dispersal and gene flow between the potential subpopulations identified. Molecular studies point to the existence of at least two lineages mostly restricted to the Adrar Atar-Tagant and Assaba mountains (Gonçalves *et al*., 2012); but additional studies are needed to determine if genetic sub-structuring occurs among the four distinct subpopulations predicted here.

Agama boulengeri was categorised as Least Concern, given that all parameters analysed exceeded the thresholds for categorization as Threatened. The species may be susceptible to climate change and natural disasters, such as drought, and quantitative data on population size and trends are needed to better estimate population parameters and assess species vulnerability to climate change.

Results from this study emphasize the biological value of Mauritanian mountains, and further support the importance of these island-like mountains for conservation of Sahelo-Saharan biodiversity (Tellería *et al*. 2008; Padial and Tellería, 2009; Trape, 2009; Brito *et al*., 2010, 2011; Vale, Álvares and Brito, 2012; Padial *et al*., in press). Distribution and habitat selection patterns observed may give indications about other mountain-restricted species in the region, with fragmented distributions and similar habitat requirements, such as *Tarentola parvicarinata*, *Pristurus adrarensis* or *Ptyodactylus ragazzi*. The methodological approach used here should be applied to other desert isolated species and particularly to other mountain endemic species.

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Chapter 5

Local hotspots of biodiversity

“What makes the desert beautiful,' said the little prince’,
is that somewhere it hides a well...”
Antoine de Saint-Exupéry, The Little Prince

ARTICLE V. OVERLOOKED MOUNTAIN ROCK POOLS IN DESERTS ARE CRITICAL LOCAL HOTSPOTS OF BIODIVERSITY[5]

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ABSTRACT

Background: The world is undergoing exceptional biodiversity loss. Most conservation efforts target biodiversity hotspots at large scales. Such approach overlooks small-sized local hotspots, which may be rich in endemic and highly threatened species. We explore the importance of mountain rock pools (gueltas) as local biodiversity hotspots in the Sahara-Sahel. Specifically, we considered how many vertebrates (total and endemics) use gueltas, what factors predict species richness, and which gueltas are of most priority for conservation. We expected to provide management recommendations, improve local biodiversity conservation, and simultaneously contribute with a framework for future enhancement of local communities' economy. The identification of local hotspots of biodiversity is important for revaluating global conservation priorities.

Methodology/Principal Findings: We quantified the number of vertebrate species from each taxonomic group and endemics present in 69 gueltas in Mauritania, then compared these with species present in a surrounding area and recorded in the country. We evaluated the predictors of species number's present in each guelta through a multiple regression model. We ranked gueltas by their priority for conservation taking into account the percentage of endemics and threats to each guelta. Within a mere aggregate extent of 43 ha, gueltas hold about 32% and 78% of the total taxa analysed and endemics of Mauritania, respectively. The number of species present in each guelta increased with the primary productivity and area of gueltas and occurrence of permanent water. Droughts and human activities threaten gueltas, while 64% of them are currently unprotected.

Conclusion/Significance: Gueltas are crucial for local biodiversity conservation and human activities. They require urgent management plans in Mauritania's mountains. They could provide refugia under climate change being important for long-term conservation of Sahara-Sahel biodiversity. Given their disproportional importance in relation to their size, they are local hotspots of biodiversity deserving global attention.

INTRODUCTION

The world is undergoing exceptional biodiversity loss [1]. Most conservation efforts target biodiversity hotspots because they constitute areas of exceptional endemic richness that are undergoing significant habitat loss [2-4]. Identification of hotspots of richness and general understanding of richness-environment relationships is of major importance. These evaluations are mostly global or continental [2], while the local patterns of species richness, endemism and rarity are less well understood [5]. Large-scale assessments are likely to miss regional patterns and small-sized areas with large number of endemics that could constitute local hotspots [6-8]. Given that most land-use transformation and management decisions are made at local or regional scales, overlooking local hotspots may constitute a serious deficiency in biodiversity conservation.

The common perception of deserts and arid regions is that they constitute remote areas of low diversity when compared to other biomes. No desert is listed in the global biodiversity hotspots [9]. In fact, the world's largest warm desert, the Sahara, together with the neighbouring arid Sahel, have patchily distributed species and a relatively high number of endemics. These species are often restricted to small and fragile humid habitats [10]. Surrounded by sandy areas, isolated and residual water features (oases, lakes and seasonal rivers) act as refugia for relict populations and constitute places where unique species evolve [10-12]. Indeed, water availability strongly predicts communities' distribution and species richness in drylands [13-14]. Desertification and human activities affect water availability and threaten these water features [10]. As such, those within the Sahara-Sahel may constitute local hotspots of biodiversity under threat. Despite the conservation importance of water features in the Sahara-Sahel, we know little about their species richness, particularly their endemics, and the threats affecting them.

In Mauritania, endemic species and range-margins populations of different biogeographic origin are restricted to mountain rock pools, locally known as gueltas [15-17]. The country is located in biogeographic crossroad between Palaearctic and Afro-tropical ecoregions [18] and mountains disrupt the latitudinal gradient in climate and habitat of the region [19]. Gueltas are small (from 0.01 to 5ha) and water availability is mostly seasonal. In many gueltas, water is only available during the rainy season (July to September), when torrential waterfalls fill up the pools [16]. This makes them susceptible to different threats and vulnerable to future climate change. The droughts of the 1970s [19-20] have caused some gueltas of northernmost Mauritania

dry out [15] and to decrease the nomadic lifestyle in favour of sedentary habits around permanent water bodies. Presently, herdsmen overexploit those gueltas, producing water-shortage during the dry season, faecal contamination by domestic animals, and increased activities for excavating pools or pumping water [16, 21]. Improved knowledge on species richness of gueltas and types of threats affecting them is important to establish priorities for their conservation.

Here, we explore the importance of gueltas as local biodiversity hotspots. We addressed three specific questions. First, how many species use gueltas? We considered how many vertebrates (total and endemics) use gueltas and compared these with those present in the mountains of Mauritania and in the country. We expected that a large proportion of vertebrates, particularly endemics, would live in gueltas. Secondly, what are the predictors of species richness? We expected that species richness would correlate with water availability. Thirdly, which gueltas are the highest priority for conservation? We identified and quantified threats to each guelta and rank gueltas according to their conservation priority. Revaluation of conservation priorities that include society needs in countries covered by deserts and arid regions are a global challenge [22]. As such, knowledge about biodiversity and threats in gueltas of Mauritania is important for local sustainable resource use that policy makers might use as framework for future enhancement of local communities' economy. The identification of local hotspots of biodiversity is important to revaluate global priorities, being a valuable contribution for global biodiversity conservation.

MATERIALS AND METHODS

ETHICS STATEMENT

Fieldwork was developed with permission from the Ministére Délégué auprès du Premier Ministre Chargé de l'Environnement, Nouakchott (Permit: 460/MDE/PNBA). This permit was valid for the entire country and no specific permissions were required for any specific locality. Analyses were done at a CITES registered laboratory: 13PT0065/S. Field collection and handling practices were approved by the Committee of Animal Experimentation of the University of Porto (Portugal) under the Directive 2010/63/EU of the European Parliament. No animal was sacrificed and there were no animal husbandry, experimentation and care/ welfare concerns.

STUDY AREA

The study area is in West Africa between 15.8ºN and 20.6ºN and west of 9.5ºW, and comprises the Mauritanian mountains of Adrar Atar, Tagant, Assaba and Afollé (Fig. 5.1). The Adrar Atar is the northernmost, with vegetation of Palearctic affinity; the harsh Sahara desert surrounds it. The southern Tagant, Assaba and Afollé mountains have wetter climate and vegetation of Sudanese affinity. Gueltas are mostly upstream of narrow valleys at the base of mountains (see C1 Appendix C). The total area occupy by gueltas in Mauritania is approximately 43 ha (0.00004 % of the total area of Mauritania and 0.0007% of its mountains).

FIELDWORK AND SPECIES OBSERVATIONS

Starting in 2007, we have completed seven overland field expeditions to Mauritania, during which we visited 69 gueltas (see C1 Table and C1 Appendix). We recorded the location and area of each guelta with a GPS (WGS84 datum). Field missions ran annually from September to December (after the rainy season), except in 2009 (March-May; dry season peak). Each guelta was sampled by at least 3 persons using several distinct methodologies: visual inspection, deep-netting, Sherman traps, camera traps, indirect observations (faeces, footprints, tracks or burrows) and night sampling of the water and margins with lamps. The effort was about 237 man-hours in total and 3.43 man-hours in each guelta. We collected 4200 geo-referenced observations from 107 vertebrates, including fishes, amphibians, reptiles and mammals. For comparison, we compiled taxonomic reference lists of vertebrates in Mauritania for fishes [15, 23-26], amphibians [27], reptiles [28], and mammals [29].

We quantified, by direct observation in the field, the type and number of threats affecting each guelta, following the nomenclature used by IUCN guidelines for listing threats [30].

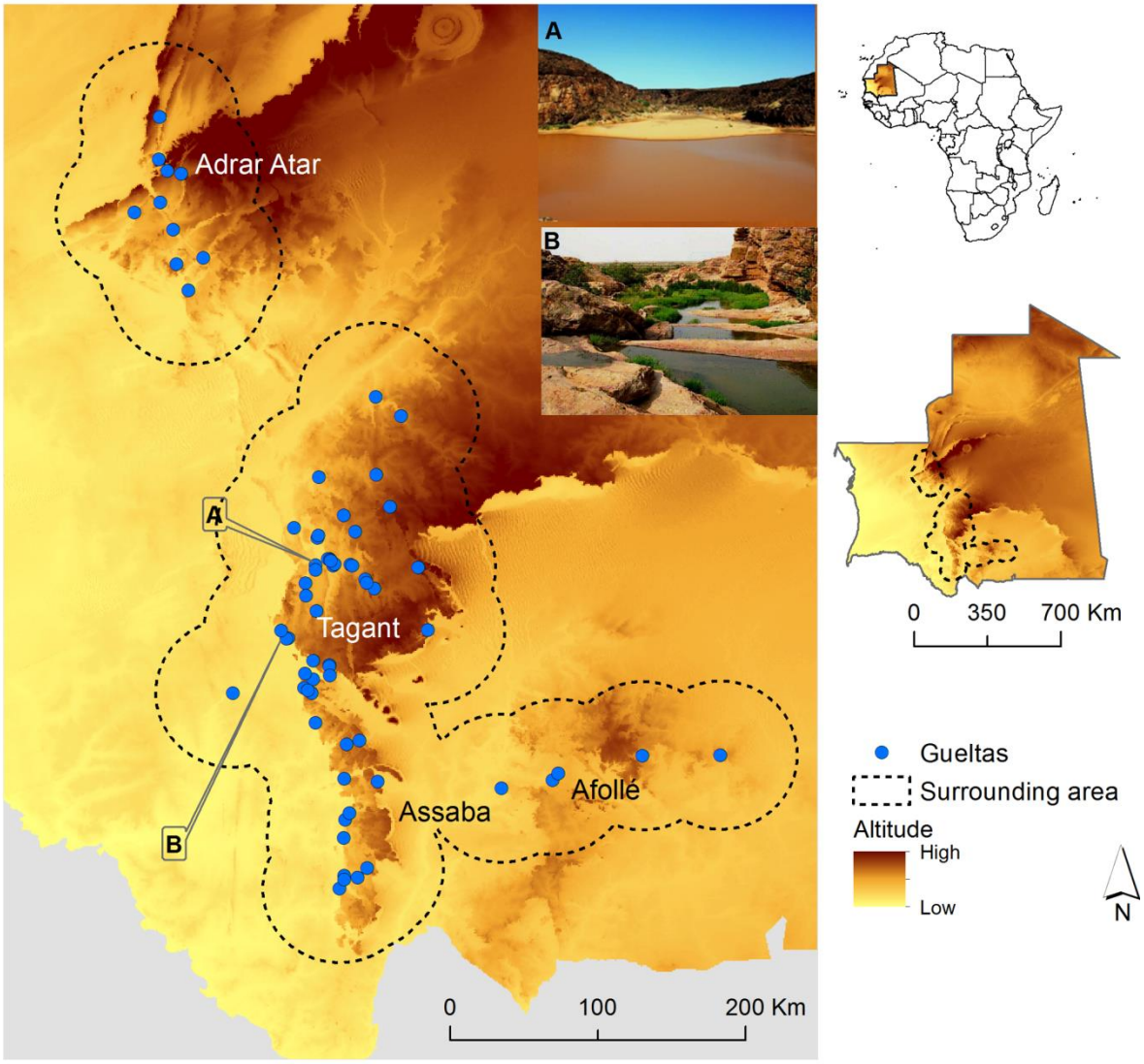

Fig. 5.1 - Study area and the locations of the gueltas. Example of two gueltas: A) Guelta Tartêga, and B) Guelta Garaouel. Black dashed line limits the surrounding area. Insets display location of Mauritania within the African context (top) and location of the surrounding area within Mauritania (bottom).

Quantification of species richness

To quantify species richness in gueltas, we first designed buffers around each guelta, using the “Buffers” tool of ArcGIS 10.0.0. Buffer size was set according to potential dispersal abilities of each taxonomic group: 2 km for fishes, amphibians and reptiles and 5 km for mammals. To quantify the number of species that occur in mountains and that could potentially reach gueltas, we defined an area that bounded gueltas with a buffer of 50km (likely corresponding to the maximum dispersal distance of any species occurring in gueltas) and call it the "surrounding area" (Fig. 5.1). We quantified the

number of species from each taxonomic group and endemics present in: 1) the gueltas; 2) in the surrounding area; and 3) in Mauritania. We then compared number of species observed in each guelta with the number of species quantified in the surrounding area, and recorded in Mauritania. We considered as Mauritanian endemics, those species with at least 75% of the global range located inside Mauritania. This includes two described species and seven taxa delimited based on genetic evidences pointing towards a reciprocally monophyletic status and long divergence time (authors' unpublished data) [31]. We used Chi-Square tests to identify significant differences in the number of species among mountains from each taxonomic group and from each IUCN conservation category.

Predictors and analyses

We selected environmental factors to evaluate their relationships with observed species richness in each guelta. They included: 1) the area of the guelta (m2) estimated in the field with a GPS (see above) 2) the Normalized Difference Water Indexes to detect permanent and seasonal water (NDWI_P and NDWI_S), respectively, at 1 arc second resolution [32]; and 3) a Normalized Difference Vegetation Index (NDVI) time-series from the period between 2003 and 2011, at 30 arc second resolution [33]. For all indexes, we calculated several measures of ecological significance: 1) annual maximum; 2) annual mean; 3) annual standard deviation; and 4) the maximum annual average. We initially explored the effects of latitude, but then excluded this variable because it so highly correlates with NDVI values ($rs > 0.80$, $p=0.00$).

We evaluated all of the predictors (including all indexes measures) of the number of species present in each guelta through a multiple regression model (GLZ), using the MuMIn package in R software v. 3.0.2. Models were ranked according to their Akaike's information criterion value. Each model's support was estimated through the difference in AICc with respect to the top-ranked model (ΔAICc). AICc rather than AIC is appropriate when there are too many parameters relative to sample size [34-35]. We used the best model to determine the importance of predictors and their significance for each model.

QUANTIFICATION OF THREAT AND CONSERVATION PRIORITIES

We ranked gueltas by their priority for conservation taking into account the percentage of endemic species and threats to each guelta. We plotted the percentage of endemics and threats and reclassified gueltas according their priority for conservation. We defined three levels of priority: 1) low - gueltas with low percentage of endemics even if they were vulnerable to high levels of threats; 2) important- gueltas with high percentage of endemics but less vulnerable to different threats; and 3) priority - gueltas with high percentage of endemics and threats. Finally, we performed Chi-Square tests to test for differences in the number of threats among gueltas of each mountain.

To quantify the number of gueltas currently protected (total and by priority levels), we intersected the location of gueltas with the protected areas of Mauritania.

RESULTS

Numbers of species

Some 59 vertebrate species use gueltas. This represents a significant portion of all vertebrates of Mauritania and of the surrounding area (Table 5.1 and see C2 Table and C3 Table). There are no significant differences in the number of species using gueltas among mountains ($p=0.93$). The number of species observed in each guelta did not increase with sampling effort ($rs =0.18$ $p=0.14$).

Gueltas held 78% of the Mauritanian endemics (Table 5.1). Gueltas of Adrar Atar exhibited fewer endemic species than gueltas of the southern mountains (Table 5.1). There are endemic species that are present in all mountains, such as *Felovia vae* (Fig. 5.2). Other endemics were restricted to the southern gueltas (*Ptyodactylus cf. togoensis* and *Hoplobatrachus cf. occipitalis*) (Fig. 5.2). The endemic Pristurus adrarensis is restricted to Adrar Atar, but it was not observed in gueltas (C2 Table).

We did not observe any species in gueltas that IUCN deems to be threatened (Table 5.1). A few species IUCN deems Data Deficient and Near Threatened species from Mauritania used gueltas, but the number increased when we compared with the species of the surrounding area (100%). A large proportion of species using gueltas remain Not Evaluated by IUCN (Table 5.1). There were no significant differences between mountains in the number of species from each IUCN conservation category ($p= 1$).

Table 5.1 - Sum of taxa (Σ) quantified in gueltas by taxonomic group and IUCN status. Sum of taxa and endemic taxa (Mau Endemic) quantified in the surrounding area (SA) and in Mauritania (Mau), and percentage of those present in gueltas (%G). DD: Data deficient; NE: Not evaluated; LC: Least concern; NT: Near threatened; VU: Vulnerable; CR: Critically Endangered.

	Σ Adrar	Σ Tagant	Σ Assaba	Σ Afollé	Σ Gueltas	Σ SA (%G)	Σ Mau (%G)
Fishes	2	2	5	3	5	7 (71)	18 (28)
Amphibians	2	3	6	3	7	7 (100)	11 (64)
Reptiles	5	16	17	10	24	41 (56)	79 (30)
Mammals	3	13	14	13	23	29 (79)	78 (29)
Total	12	34	42	29	59	86 (69)	186 (32)
Mau Endemic	2	5	6	4	7	9 (78)	9 (78)
DD	1	2	2	2	2	3 (67)	7 (29)
NE	5	13	18	11	23	40 (58)	69 (33)
LC	6	18	21	15	33	40 (83)	96 (34)
NT	0	1	1	1	1	1 (100)	6 (17)
VU	0	0	0	0	0	2 (0)	7 (0)
CR	0	0	0	0	0	0 (0)	1 (0)

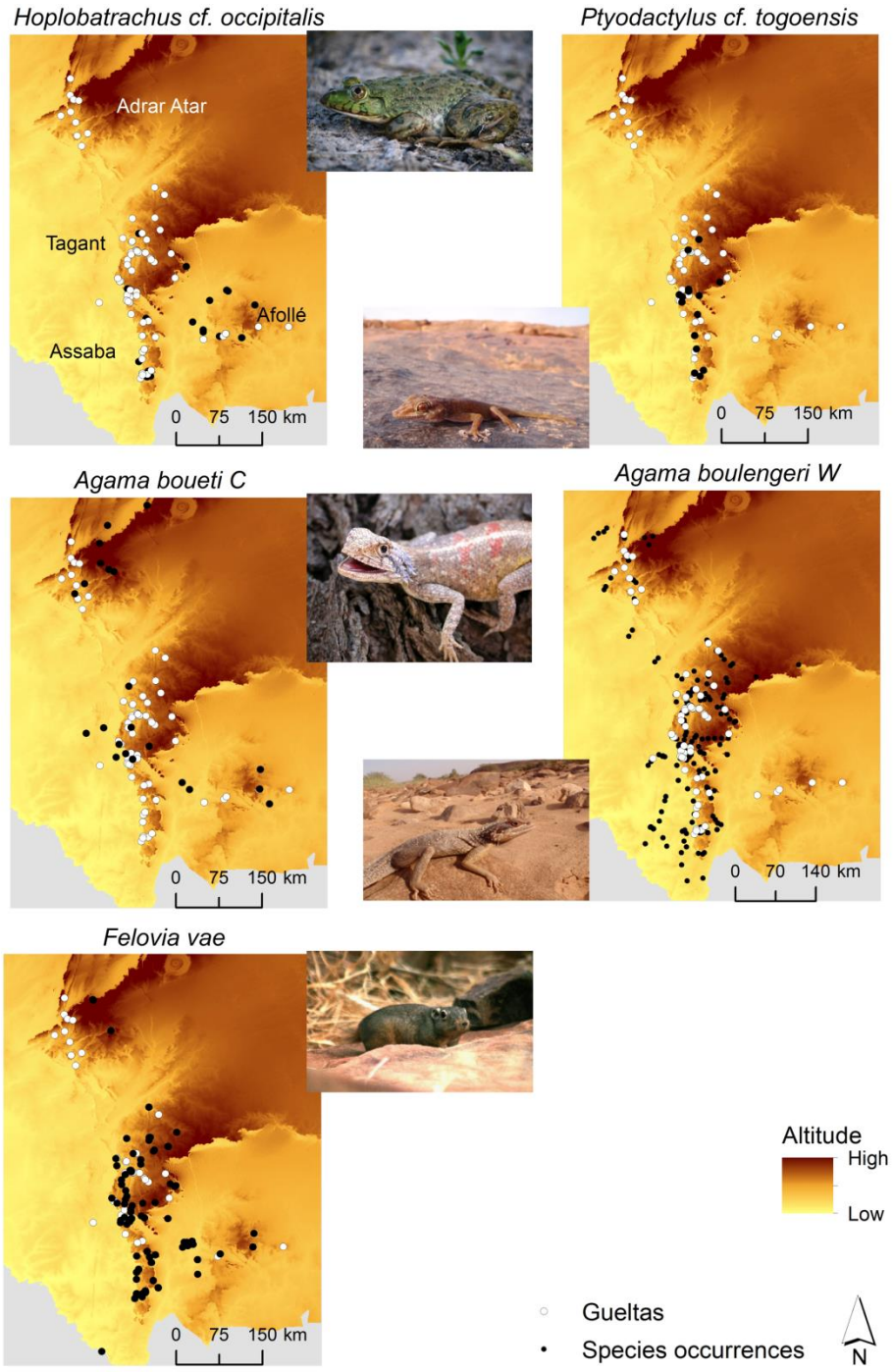

Fig. 5.2 - Known distribution of endemic taxa of Mauritania observed in gueltas.

PREDICTORS OF THE NUMBERS OF SPECIES, QUANTIFICATION OF THREATS AND CONSERVATION PRIORITIES

We selected the best model to describe relationships between species richness and predictors according to the lower AICc (Table 5.2). The number of species present in each guelta increased with both productivity (maximum of the annual average NDVI), occurrence of permanent water (annual average NDWI_P), and area of the guelta, and declined with the occurrence of seasonal water (maximum NDWI_S; Table 2). Droughts and temperature extremes threatened all gueltas (100%, Table 5.3) and extraction of water for domestic use and nomadic grazing were also frequent (81% and 80%, respectively). There were no significant differences between mountains in the number of threats observed in each guelta (p= 0.504). Human related threats increase with the increasing area of gueltas (rs =0.3, p=0.01).

There were significant differences in priorities for conservation between gueltas in each mountain (p=0.009). The most priority gueltas for conservation were located in the southern mountains: Tagant, Assaba and Afollé (Fig. 5.3). From the 69 gueltas, only 25 are currently included in one Ramsar site in the Tagant plateau while remaining gueltas (~64%) do not have any legal protection status. From the 25 gueltas protected by the Ramsar site, 16% and 12% were ranked as priority and important for conservation, respectively. About 80% of the gueltas (N=16) identified as priorities are unprotected.

Table 5.2 - Measures of the predictors most related with the species richness in gueltas (GLZ). Significance codes: p < 0.0001 ***; p < 0.001 **; p < 0.01 *. NDVImax_avg: Maximum of the annual average of Normalized Difference Vegetation Index; NDWI_Pavg and NDWI_Psd: Annual average and standard deviation of the annual average of Normalized Difference Water Indexes of permanent water, respectively; and NDWI_Smax: Maximum of Normalized Difference Water Index of seasonal water.

	β	Std. Error	z value	Pr(>|z|)	AICc	ΔAIC	Wi
AREA	0.00	0.00	2.76	0.01**			
NDVImax_avg	0.00	0.00	6.15	0.00***			
NDWI_Pavg	6.70	1.60	4.19	0.00***	379.87	0	0.23
NDWI_Psd	4.85	1.97	2.47	0.01*			
NDWI_Smax	-3.16	0.69	-4.57	0.00***			

Table 5.3 - Number and percentage of gueltas affected by each threat. Codes follow the IUCN Threats Classification Scheme [30].

Threats		Σ Gueltas (%)
2.3.1	Nomadic grazing	55 (80)
2.3.2	Small-holder grazing, ranching or farming	24 (35)
5.1.1	Intentional use (species being assessed is the target)	10 (14)
5.4.1	Intentional use: subsistence/small scale (species being assessed is the target)	24 (35)
7.2.1	Abstraction of surface water (domestic use)	56 (81)
7.2.3	Abstraction of surface water (agricultural use)	21 (30)
9.3.4	Pollution: Type Unknown/Unrecorded	51 (74)
9.4	Pollution: Garbage & solid waste	23 (33)
10.3	Avalanches/landslides	26 (38)
11.2	Droughts	69 (100)
11.3	Temperature extremes	69 (100)

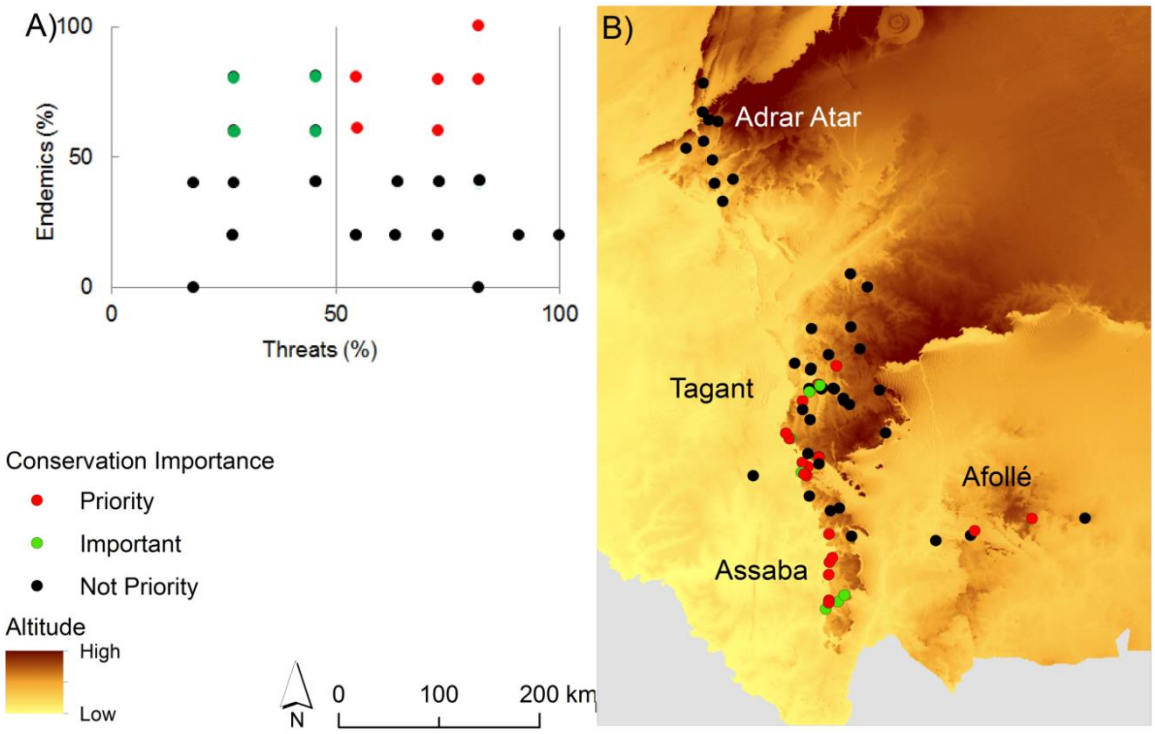

Fig. 5.3 Priority gueltas for conservation. A) Ranking of conservation importance of gueltas taking into account the percentage of endemics and threats. Red dots represent priority gueltas for conservation (many endemics and threats); green dots represent important gueltas for conservation (many endemics and few threats) and black dots represent less important gueltas for conservation (few endemics). B) Location of all gueltas coloured by the importance for conservation.

DISCUSSION

Gueltas are special places and are disproportionately important for their tiny size. The 69 gueltas contained 32% of the analysed vertebrates of Mauritania and 78% of the country's endemics in an area representing only 0.00004% of the country. As such, gueltas are local hotspots of biodiversity deserving global attention. IUCN deems none of the species as threatened, but a large proportion has not yet been evaluated. The observed lack of threatened species may reflect knowledge gaps about desert biodiversity [10], suggesting that we need more complete evaluations of conservation status.

The number of endemics is not similar in each mountain. The gueltas of southern mountains house more endemic species in comparison to the gueltas of Adrar Atar. For instance, the amphibian Hoplobatrachus cf. occipitalis is apparently restricted to the southern mountains. Lower diversity of endemics in Adrar Atar may be related to latitudinal gradients in climate and habitat, environmental tolerances of each species, and past Sahara-Sahel climatic oscillations [10]. These oscillations induced a series of extinctions and recolonizations and perhaps adaptation events that have shaped species composition in each mountain. Several species from Afro-tropical region have expanded throughout the Sahara-Sahel during wetter periods and then remained in mountain refugia during dry periods [10]. Currently, gueltas are refugia for several species due to the region's aridity. Yet, these aquatic systems, as evolutionary and ecological refuges in arid environments are likely to constitute future refuges under global and regional climatic changes [36]. As future climate models predict more frequent or severe droughts for the region [20, 37], it is likely that gueltas will also constitute refugia under future climate change, particularly for water-dependent species.

High primary productivity, presence of permanent water, and area of gueltas are the best predictors of the numbers of species. Given the harsh surrounding environment, gueltas with high primary productivity likely held more species, as the amount of energy available is a major determinant of species richness [38]. Studies made in permanent and ephemeral streams subjected have found strong correlations between specie's numbers and maximum NDVI [38]. Larger gueltas likely create opportunities and habitat conditions for more species. Permanent water is important for fishes, crocodiles and mammals in the gueltas of Mauritania [10, 15, 17] as well as for relict populations of Afro-tropical fishes in the gueltas of the Tibesti mountain of Chad [12]. In

fact, gueltas could be the only source of water over large distances across the Sahara-Sahel. Permanent water features play a vital role in the conservation of local biodiversity, particularly in arid environments worldwide [36]. Research efforts should quantify species richness and threats in gueltas in other Sahara-Sahel mountains [10].

Droughts and temperature extremes affect all gueltas. Human disturbance is important and larger gueltas are more vulnerable to human pressures. Local communities base their economy on the exploration of the water and surrounding habitats of gueltas. Rock engravings provide clear historical evidences of their human use since the Neolithic [39]. Moreover, human activities in gueltas likely increased after the droughts of 1970's. As an example, the Tagant plateau currently houses a population of agriculturalists and herdsmen, leading to activities of excavating pools and pumping water and to faecal contamination of water [21, 39]. The importance of gueltas for both biodiversity conservation and human activities suggest that the conservation of these local hotspots should incorporate the management of water as a resource.

The southern mountains (Tagant, Assaba and Afollé) hold the gueltas with the highest concentrations of endemics and, at the same time, the most threatened gueltas. The importance of the Tagant plateau has been recognized and the "Lac Gabou et le Réseau Hydrographique du Plateau du Tagant" have been classified as a Ramsar site [39]. The site only covers 20% of the top-priority gueltas for conservation, however. In fact, 64% of the total gueltas are unprotected and the current protected area network of the country fails to adequately preserve gueltas and its biodiversity. Designation of more protected areas should be considered for the gueltas this study identifies as most important.

Gueltas are special places for the conservation of biodiversity and simultaneously crucial for local communities activities. Mauritania is listed by FAO as of Low-Income Food-Deficit Country [40] and its Gross national income (GNI) per capita was 2.118 $US in 2010 (for instance: USA was 47.094 $US [41]). Livestock play an important role in the country, contributing around 10–15% of the GNI of the country [42]. As such, the allocation of land to biodiversity conservation competes with other land uses and societal needs. We believe that the best strategy to protect gueltas is to rank priorities for conservation and design a reserve network that would enhance both the protection of biodiversity and a sustainable development. Mauritania has been listed among the top countries with highest return-on-investment [43]. A conservation plan should reveal the economic benefits and rewards that local communities can derive from ecosystem services, such as sustainable resource use, ecotourism, and public health. For instance, conduction channels could feed troughs distant from the guelta, thus reducing current human and livestock pressure. Such infrastructures would also allow

decreasing faecal contamination of the water, contributing to public health. Pollution threatens water quality in Mauritania [44] and diarrhoea is prevalent in the south of the country [45]. Organised ecotourism is possible, as the most accessible gueltas have crocodiles (particularly at Matmâta, see C1 Appendix) and groups of travellers regularly visit the ruins of Ksar el Barka [39]. To meet these proposals, funds might be obtained from the Global Environment Facility of the World Bank. Combining conservation priorities that factor in both biodiversity value and conservation management investments provides a new lens for setting global conservation priorities [43]. As such, a conservation programme should be implemented to protected these local hotspots and therefore, improve global biodiversity conservation.

Our study demonstrates the importance of gueltas as local biodiversity hotspots and it lays the foundations to build an effective conservation plan to protect them. Due to the current lack of information, complementary studies are still needed. The taxonomy and systematics of many reptiles and fishes is still uncertain, and molecular tools should be applied to identify conservation units. Often allied with water pools in deserts, aquatic macro invertebrates and bats also need further investigation. As aquatic macro invertebrates are considered good indicators of water quality in arid environments [46], their identification could also contribute to manage potential disease-vector species in gueltas. Physicochemical parameters (i.e. temperature, pH, conductivity, dissolved oxygen and turbidity); nitrates and nitrites concentrations, organic suspend matter and concentrations of chlorophyll a (a measure of algal biomass) should also be conducted to quantify water quality parameters related to public health. Studies about aquatic flora are also required.

CONCLUSION

Gueltas are tiny places that hold high number of species, including endemics, and they are vulnerable to droughts and human activities. Given their disproportional importance for their size, they constitute local hotspots of biodiversity, overlooked by global assessments. Moreover, they could provide refugia under climate change, so they are crucial for long-term conservation of Sahara-Sahel biodiversity. Reserve networks that enhance both biodiversity conservation and human activities should be implemented in Mauritanian mountains. The observed value of gueltas of Mauritania as local hotspots are well representative of all gueltas of the Sahara-Sahel mountains as well as other small yet rich places surrounded by hostile habitats.

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Chapter 6

Sahara-Sahel functional groups vulnerability to future climate change

"If this is not done, future ages will certainly look back upon us as a people so immersed in the pursuit of wealth as to be blind to higher considerations."
(From Alfred Russell Wallace's 1863 article On the physical geography of the Malay Archipelago. *Journal of the Royal Geographical Society* 33: 217-234).

ARTICLE VI. DESERT-ADAPTED SPECIES ARE VULNERABLE TO CLIMATE CHANGE: INSIGHTS FROM THE WARMEST REGION ON EARTH[6]

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ABSTRACT

Climate change is eroding biodiversity and conservation efforts have focused on species' potential responses to those changes. Biological traits associated with sensitivity and adaptive capacities may contribute in identifying a species vulnerability to climate change. Desert-living species could be particularly vulnerable to climate change as they may already live at their physiological limits. This work aims to identify functional groups in Sahara-Sahel endemics, to determine their spatial distribution and to evaluate how the predicted magnitude and velocity of climate change in the region might affect them. We collated biological traits data for all Sahara-Sahel endemics. We then summarized the functional strategy of each species into functional groups with different sensitivities and adaptive capacities to climate change. Future climate scenarios were reclassified to identify areas where predicted temperature and precipitation approach the physiological limits of each group. We calculated the velocity of temperature and precipitation change as the ratio of the temporal gradient to the spatial gradient. Specific magnitudes and velocities of environmental change threaten our seven function groups differently according to their level of exposure and geographical distributions. Groups are more exposed to precipitation than to temperature changes. The more exposed functional groups lived mostly in flat areas, where the predicted magnitude and velocities of change were also the highest. Some functional groups with high adaptive abilities (e.g. volant species) may be able to colonize distinct areas. Other groups with low sensitivity and adaptive capacity (e.g.: ectotherms with small home ranges) may be vulnerable to climate change. Different biological traits contributed to the extent to which climate change harms species. The desert-adapted species may be the most vulnerable ones. The vulnerability patterns of Sahara-Sahel functional groups provide indications of combinations of biological traits and biodiversity's exposure to climate change in other warm deserts of the world.

Keywords: Adaptive capacity; exposure; functional groups; magnitude; sensitivity; velocity of climate change

INTRODUCTION

Climate change is widely accepted as a major threat to biodiversity, with potential to accelerate the pace of its loss (Bellard *et al*., 2014). We need accurate forecasts of climate change effects on biodiversity to design the most proactive conservation strategies. Most current assessments of its potential impacts are focused either on changes in the geographical extent of species' climate space or changes in the exposure of areas to different dimensions of climate change. Yet, models focused on changes in the species' distribution fail to explicitly reflect the broad range of climate-induced stress affecting populations' ecology and species' physiology (Foden *et al*., 2013; Willis *et al*., 2015). Studies rarely appreciate the quantifications of areas exposed to the different dimensions of climate change in combination, despite their different implications for biodiversity (Garcia *et al*. 2014). For instance, decreasing local climate suitability (magnitude) may threaten species living close to their upper climatic tolerance limits, and high velocities of climate change may affect the ability of species to track suitable climatic conditions, particularly those with low dispersal abilities (Garcia *et al*. 2014). As such, climate change' assessments and identification of the most vulnerable species would profit from the incorporation of biological traits and combined analyse of the effects of different dimensions of climate change.

Rapidly changing climate will likely alter the selective pressures acting on species. Species vulnerability to these changes will yet depend on their level of exposure. That is, to what extent will their geographical environment space change their sensitivity, i.e. the lack of potential for a species to persist *in situ*. And how will it affect their adaptive capacity, i.e. the species' inability to avoid the harmful impacts of climate change through dispersal or micro-evolutionary change (Foden *et al*., 2013; Moritz and Agudo 2013; Willis *et al*., 2015). Among other biological traits correlated with species extinction risk, those related with sensitivity include thermoregulation, activity, habitat specialisation, reproduction, and ecological plasticity. Those related with adaptive capacity include dispersal ability and body size (Brook *et al*. 2008; Kearney 2013; Pincheira-Donoso *et al* 2013; Bennie *et al*., 2014; McCain and King, 2014; Buckley *et al* 2015). For instance, diurnal ectotherms may be particularly sensitive to temperature changes, as they regulate body temperature directly from external sources and simultaneously present low adaptive capacity due to relatively sedentary behaviour and small home ranges (Barrows *et al*., 2011). Increasing body size and activity time in mammals strongly relate to local extirpations, range contractions, and population declines (McCain and King, 2014). Beside species' evolutionary history (e.g.: its exposure to past climate fluctuations) and physiological plasticity or acclimation

increase their resilience to environmental fluctuations; the magnitude of future climate change may outstrip species' sensitivity and adaptive capacity (Seebacher *et al*., 2014). Moreover, species living in flat areas are potentially more exposed to climate change as high change velocities are higher there (Loarie *et al*., 2009). For species to persist they will need to keep pace with the moving climate, and exhibit high adaptive capacities, such as dispersal (Walther *et al*., 2002; Massot *et al*., 2008). As such, the magnitude and velocity climate change will have fundamentally different impacts depending on the species adaptive and dispersal capacities.

Deserts and arid regions harbour unexpectedly high diversity of species subject to a strong climatic control (Ward *et al*., 2009). Due to convergent evolution of biological traits and/or adaptive processes, desert species exhibit unique morphological, physiological and/or behavioural adaptations to climatic extremes (Murphy *et al*., 2012, 2013; Wilson and Pitts, 2012, Brito *et al*., 2014). Despite of this, they may be sensitive to increasing temperature, due to physiological limits constraining the evolution of species' tolerances to high temperatures (Araújo *et al*., 2013). Furthermore, in arid environments, changes in precipitation might have even more dramatic impacts on biodiversity in comparison to other ecosystems. Precipitation changes affects species as it promotes germination and food and water supply (Beatley, 1969; Pianka, 1970; Brown and Ernest, 2002). Moreover, in warming areas, rainfall fluctuations stimulate evaporation or soil warming, promoting aridity (Ward, 2009; Sherwood and Fu, 2014). Indeed, the impact of the progressive aridity conditions on arid adapted species have been already observed by negative population trends, extinctions and range shifts in the Sahara-Sahel (Trape, 2009; Brito *et al*., 2014). The region displays high topographical and climatic heterogeneity and has experienced recent and strong climatic oscillations (Wang *et al*., 2008; Claussen, 2009; Brito *et al*., 2014). Such fluctuations have greatly shaped land-cover and biodiversity distribution (Dumont, 1982; Le Houérou, 1992, 1997; Drake *et al*., 2011), suggesting that the predicted strong and fast climate changes for the region (IPCC, 2013; Loarie *et al*., 2009) will threat its biodiversity. Although, Sahara-Sahel endemics are arid-adapted species, they might be sensitive to temperature and precipitation changes, or have a capacity to handle to the predicted changes. Thus, we should identify the groups of species that combine biological traits related to vulnerability to different dimensions of climatic change. Their identification will allow designing future conservation plans for Sahara-Sahel biodiversity under climate change.

Our main goal is to identify the most vulnerable functional groups in the Sahara-Sahel under future climate changes, by addressing four questions: i) which functional groups are more vulnerable to magnitude of climate change; ii) which functional groups will

likely be able to keep pace with predicted velocity of climate change; iii) where are located the potentially most vulnerable areas? and iv) how are the most vulnerable functional groups represented within the current protected areas network? We hypothesise that functional groups comprising diurnal ectotherms with low adaptive capacities (e.g.: small home range and body size) should be most vulnerable to changes in the magnitude and velocity of temperature while groups containing endotherms with low adaptive capacity (low dispersal ability) should be most vulnerable to changes in precipitation. Functional groups harbouring taxa simultaneously sensitive and with low adaptive capacity and living in flat areas are expected to be more vulnerable to the velocity of climate change. The identification of functional groups and their potential vulnerability to climate change are essential to design proactive conservation plans for Sahara-Sahel biodiversity.

METHODS

Our study area covers a total of ≈11,200,000 km2 and includes the Sahara (≈8,200,000 km2) and Sahel (≈3,000,000 km2), as defined by Olson *et al*., (2001) (Fig. 6.1). We have divided the study area into 4,417 grid cells, using a grid of ~54km (~0.5º) resolution projected to Africa Albers Equal Area Conic projection.

DISTRIBUTION DATA AND FUNCTIONAL TRAITS

The total list of endemics vertebrates (125 species) occurring in the Sahara-Sahel was retrieved from IUCN (2013) and BirdLife International and NatureServe (2011) databases (97 terrestrial amphibians, reptiles and mammals and birds) and further supplemented with local distribution data from published atlases (28 reptiles; Sindaco and Jeremčenko, 2008; Sindaco *et al*., 2013). We have considered species with at least 75% of their range overlapping the study area as endemics or nearly endemic species of the Sahara-Sahel. Polygons of species distribution were intersected with a grid of grid of ~54km (~0.5º) degree resolution to generate matrices of species presence/absence by grid cell.

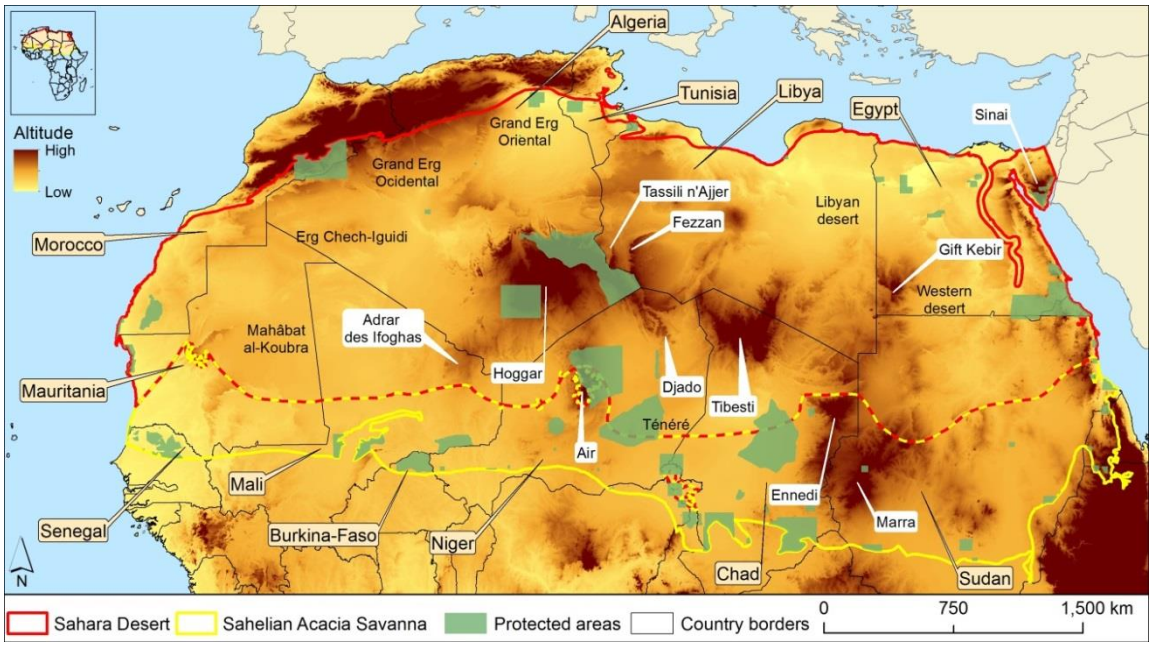

Fig. 6.1 - The Sahara-Sahel study area. Limits of the Sahara-Sahel (Olson *et al.,* 2001) and distribution of protected areas (green). Countries names are in pink balloons. Main mountain names (white balloons) and empty quarters of the Sahara-Sahel used in the text.

We described the functional strategy of each species using two main categories: sensitivity and adaptive capacity. These are thought to be mostly closely related with responses to climate change (Foden *et al*., 2013). Given that there is no information about physiological traits for Sahara-Sahel endemics, we used surrogate biological traits related with species extinction risk (Brook *et al*. 2008; Kearney 2013; Pincheira-Donoso *et al* 2013; Bennie *et al*., 2014; McCain *et al*. 2014; Buckley *et al* 2015). We collated information for each species biological trait from bibliography, public databases and expert knowledge (List D.1 in Appendix D). Sensitivity was described using seven categorical traits: 1) Thermoregulation, coded as ectothermic or endothermic; 2) Water dependency in some stage of life cycle, coded as yes or no; 3) Habitat selection, coded as presence/ absence in vegetated areas, bare areas, rocky outcrops, and/or sandy areas; 4) Activity, coded for simplicity as nocturnal or diurnal; 5) Reproduction, coded as oviparity or viviparity; 6) Diet, coded as omnivorous, carnivorous, insectivorous or herbivorous; and 7) Ecological plasticity, given by the number of ecoregions were the species were is present, ranging from one to seven (Brito *et al*., *in prep*). Adaptive ability was described using three biological traits: 1) home range size, coded using categories: <1 km2; 1 – 5; 5-10; 10 – 20; 20 - 40; and >40km2); 2) Body size (cm), which was a continuous variable; and 3) Volant, coded as yes or no.

To estimate the level of redundancy among biological traits, we used a correlation test to each pair of biological traits. We first created a distance matrix for each biological trait, using Gower distance, as most of the variables are nominal (Gower, 1971, Podani, 1999). We performed a Mantel test with the Spearman rank correlation method between every possible pair of distance matrices, using the package Vegan implemented in R. All biological traits had correlations values below 0.432, with the only exception of Thermoregulation and Reproduction (ρ=0.677; Table D.1 in Appendix D).

IDENTIFICATION OF FUNCTIONAL GROUPS

We have computed a pairwise differences matrix between species using Gower distance, which allows mixing different types of variables (Gower, 1971, Podani, 1999). Given that the importance of each biological trait is unknown a priori, we gave equal weights to each. As habitat selection is a qualitative biological trait for which a species could have more than one attribute (e.g. they could occur both in bare and rocky areas) different weights are required (Laliberté and Legendre, 2010). We have assumed a weight $w_i = x_i/b_i$ to each binary variable (e.g. presence/absence in bare areas) required to reclassify the main trait (Habitat selection), where x_i is the original weight given to the main biological trait i and b_i is the number of binary variables required to re-code trait i (Laliberté and Legendre, 2010). We used the "k-means" method and the Simple Structure index (SSI) to estimate the number of functional groups and functional group richness. To estimate the independent contributions of each biological trait to the global Gower's distance, we correlated squared distance matrices for each trait with the global squared distance (Pavoine *et al*., 2009). A Principal Coordinates Analysis (PCoA) using Gower distance matrix was calculated to locate each functional group in the multidimensional trait space. The resulting PCoA axes were taken as new "traits" to calculate the volume of the multidimensional trait space occupied by species within the functional space. The multidimensional trait space of each functional group was the minimum convex hull that includes all species from each functional group (Villéger *et al*., 2008). As negative PCoA cannot be represented in a Euclidean space, we have applied a Cailliez correction (Cailliez, 1983). As dimension reduction was required, only two PCoA axes were used to define the minimum convex hull for all. All analysis were performed within R environment (version 3.1.1), with the FD package, version 1.0-12 (Laliberté *et al*., 2014).

To test if the number of functional groups differs from what we expect if we selected species at random, we performed a simulation approach to create null distributions of

Functional Group Richness (FGR) for a given species richness value. We randomly selected species from the total number of species richness, and performed 999 replicates to produce a final median null distribution of the FGR values. Based on the null distributions, we calculated the standard effective size (SES) for each pixel (~0.5º) to measure the deviation of the observed value from the mean of the null distribution, but removing the directional bias associated with the decrease in variance in the expected values with increasing species richness (Swenson, 2014). P-values were calculated to test our null hypothesis: the number of functional groups in each pixel does not differ from what one expects by chance. For negative values of SES, FGR is lower than expected by chance and positive SES, the opposite. We used the same simulation approach to test if the patterns of each functional group are constant if we selected species at random.

Each observed group richness was converted into percentage of group richness in relation to the total species richness by pixel. This was done to access presentation of each group by pixel. To access the current extent of each group we reclassified latter maps, in order to ensure 50% of representativeness of each group by pixel. For groups with distribution skewed to the low values, we retained 75% as the distribution of the values.

CLIMATE DATA AND ANALYSIS

For current and future climate data we used 30-arcsecWorldClim Annual Mean Temperature and Total Annual Precipitation bioclimatic variables (http://www.worldclim.org/). Future variables were download for two time periods available 2041-2060 and 2061-2081 (hereafter referred as: 2050s and 2080s, respectively), based on two greenhouse gas concentration trajectories or representative concentration pathways (RCP4.5 and RCP 8.5) implemented by ten general circulation models (GCMs) of the Coupled Model Intercomparison Project Phase 5 (CMIP5) multi model dataset: CCSM4, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MRI-CGCM3 and NorESM1-M adopted by the IPCC for its fifth Assessment Report (AR5) (IPCC, 2013).We excluded GCMs for which all RCPs were not available, with the exception of BCC-CSM1-1 that was excluded due to artefacts detected in one of the variables. Representative Concentration Pathways (RCPs) are four greenhouse gas concentration and we used only the RCP 4.5 and RCP 8.5 in order to test two extreme scenarios. All variables for all time periods were projected to Africa Albers Equal Area Conic and upscale to ~54km (~0.5º).

We summarize the 10 GCMs, into mean, upper and lower projection by calculating the mean and the mean +/- s.d. of the 10 GCMs for 2080s and for each pathway (see Fig. D.1 in Appendix D). To identify areas where each functional group might be more exposed to climate change, we reclassified the mean, upper and lower projections and overlapped them with each functional group extent. To reclassify the temperature projections, we applied lower critical temperatures observed for reptiles, mammals, and birds as threshold and according to each functional group (mean – s.d., according to Araújo *et al*., 2013). We applied the lower values, as the maximum of the annual mean temperature predicted for the study area is lower than the mean critical values. To reclassify the precipitation projections, we used the value for classifying arid environments (200 mm; Greve *et al*., 2011). Latter reclassifications have resulted in binary maps for each functional group classifying areas above and below critical temperatures and precipitations.

We have computed the velocity of climate change for both mean annual temperature (º C) and total annual precipitation (mm) as the ratio of the temporal gradient to the spatial gradient (Loarie *et al*., 2009). To compute temporal gradients, we first calculate separate slopes for each pixel from each of the 10 separate GCMs time series and for the two pathways, using linear regression. To calculate the spatial gradient, from the current climate maps, we calculated spatial gradients from a 3x3 grid cell neighbourhood using the average maximum technique. We calculated the velocity of climate change for each pathway and for the 10 separate GCMs, and summarized into the mean velocity of climate change. We plotted the histograms of the velocity of climate change for each functional group extent of occupancy and compared with the mean velocity of climate change of each group.

RESULTS

We identified seven functional groups in the Sahara-Sahel based on the Gower distance matrix between species traits (Fig. 6.2; Table D.2 in Appendix D) and reproduction and thermoregulation were the traits with higher independent contribution to the global mean distance (0.69 and 0.68, respectively; Table D.3 in Appendix D). EctNocS is mostly nocturnal ectotherms, mostly insectivorous with small home ranges ; EndNocS grouped small mammals, mostly nocturnal and omnivorous, with small home ranges; EndNocM grouped nocturnal endotherms with medium to high home ranges; EctDiuM had diurnal reptiles with medium home ranges; EndDiuL grouped diurnal endotherms, herbivorous and with moderate to high home ranges; EndDiuS

included birds with small home ranges; and EctDiuS is mostly constituted of lizards, which are diurnal ectotherms with small home ranges (Fig. 6.2; Table D.2 in Appendix D).

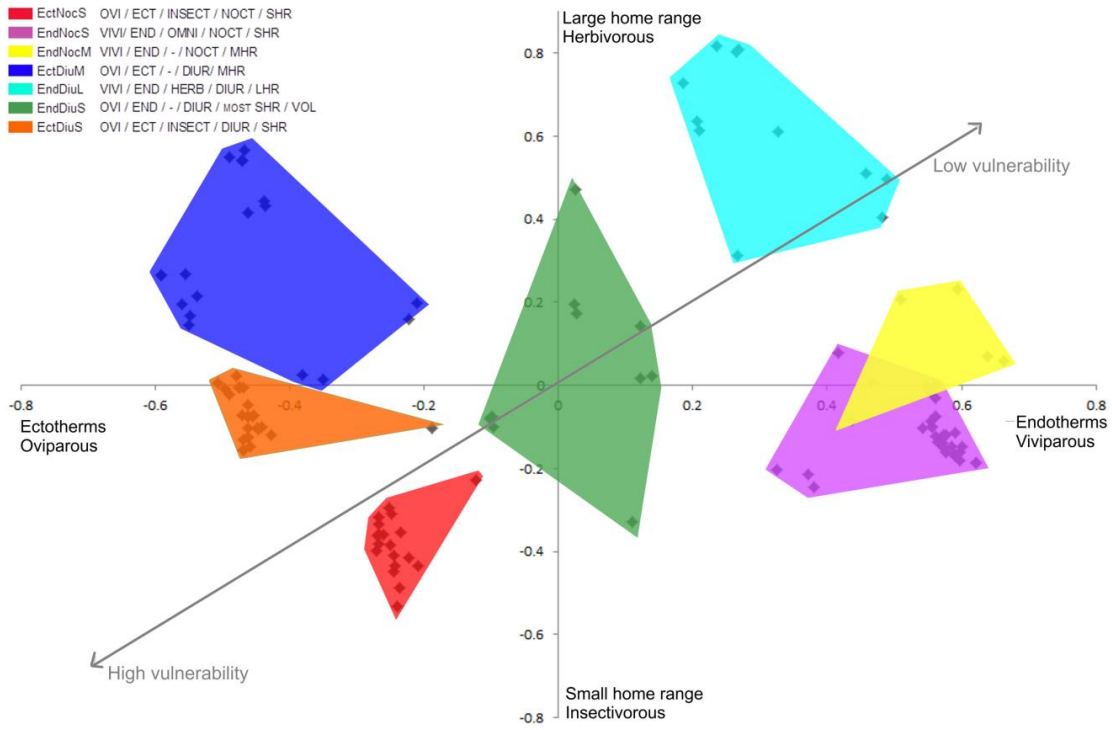

Fig. 6.2 - Minimum convex hull of Sahara-Sahel functional group derived from a pairwise distance matrix between species traits and summarized in the first two axes of a PCoA. Groups characterized by the traits: OVI - oviparous; VIVI – viviparous; END - endotherms; ECT – ectotherms; INSECT - mostly insectivorous; OMNI - mostly omnivorous; HERB – herbivorous; NOCT – nocturnal; DIUR - diurnal; SHR - small home range; LHR - large home range; VOL - volant.

Functional group richness was a function of species richness. It does not significantly differ from what one expects from species richness (see Fig. D.2, in Appendix D). The observed number of function groups in each pixel was not significantly different than averaged expected by chance (max =8, p > 0.5 Fig. D.2, in Appendix D). The same was observed for the pattern of each group, as species consistently grouped with the same species (p>0.05, Fig. D.3, in Appendix D).

Functional groups exhibited different distribution patterns across the Sahara-Sahel (Fig. 6.3): i) from wide distribution covering both Sahara and Sahel ecoregions (EctNocS; EndNocS; EndNocM; EctDiuM and EndDiuL) to restricted to one of the ecoregions (EndDiuS to the Sahel and EctDiuS to the Sahara); and ii) from distribution across the lowland areas (EndNocS and EctDiuS) to restricted to mountain ranges (EndNocM and EndDiuL). Groups were potentially exposed to distinct magnitudes of

temperature and precipitation changes according to their range (Fig 6.4): i) most groups were affected principally by changes in precipitation rather than by temperature (EctNocS, EctDiuM, EndDiuL and EctDiuS). EndDiuS was most susceptible to temperature changes (Fig 6.4 and Fig. D.1; Table D.4 in Appendix D); ii) Two groups (EndNocS and EndNocM) were affected by both precipitation and temperature changes in almost the same proportions (Fig 6.4 and Fig. D.1; Table D.4 in Appendix D); iii) There were groups (EndNocS, EctDiuM, EndDiuL and EctDiuS) that were exposed in all their extent of occurrence, while other groups (EctNocS, EndNocM and EndDiuS) were only sensible in parts of their extent (Table D.4); iv) Areas of exposure to both precipitation and temperature changes were in the transition between Sahara-Sahel (affecting EndNocS, EndNocM, EndDiuS and EctDiuS).

Groups were more exposed to velocity of change in precipitation according to their range in comparison to temperature velocity (Fig. 6.5). The overall distribution of values of velocity of temperature change in each group range was below the mean values of velocity for each group. In contrast, the values of velocity of precipitation change in EndNocS, EndNocM, EndDiuS and EctDiuS was skewed suggesting vulnerability to precipitation change.

From the total range of each functional group only less than 11% is located in currently protected areas (Table D.4). Overall, less than 8% of the potentially vulnerable areas were located in protected areas. No more than 1% of the exposed ranges of groups EctNocS, EndNocS, EctDiuM, and EctDiuS to temperature change are currently protected, and less than 3% of the exposure areas of groups EctNocS, EndNocM and EndDiuS to precipitation changes are located within protected areas. Less than 3.4% of the range of groups potentially not exposed to climate change is located in current protected areas.

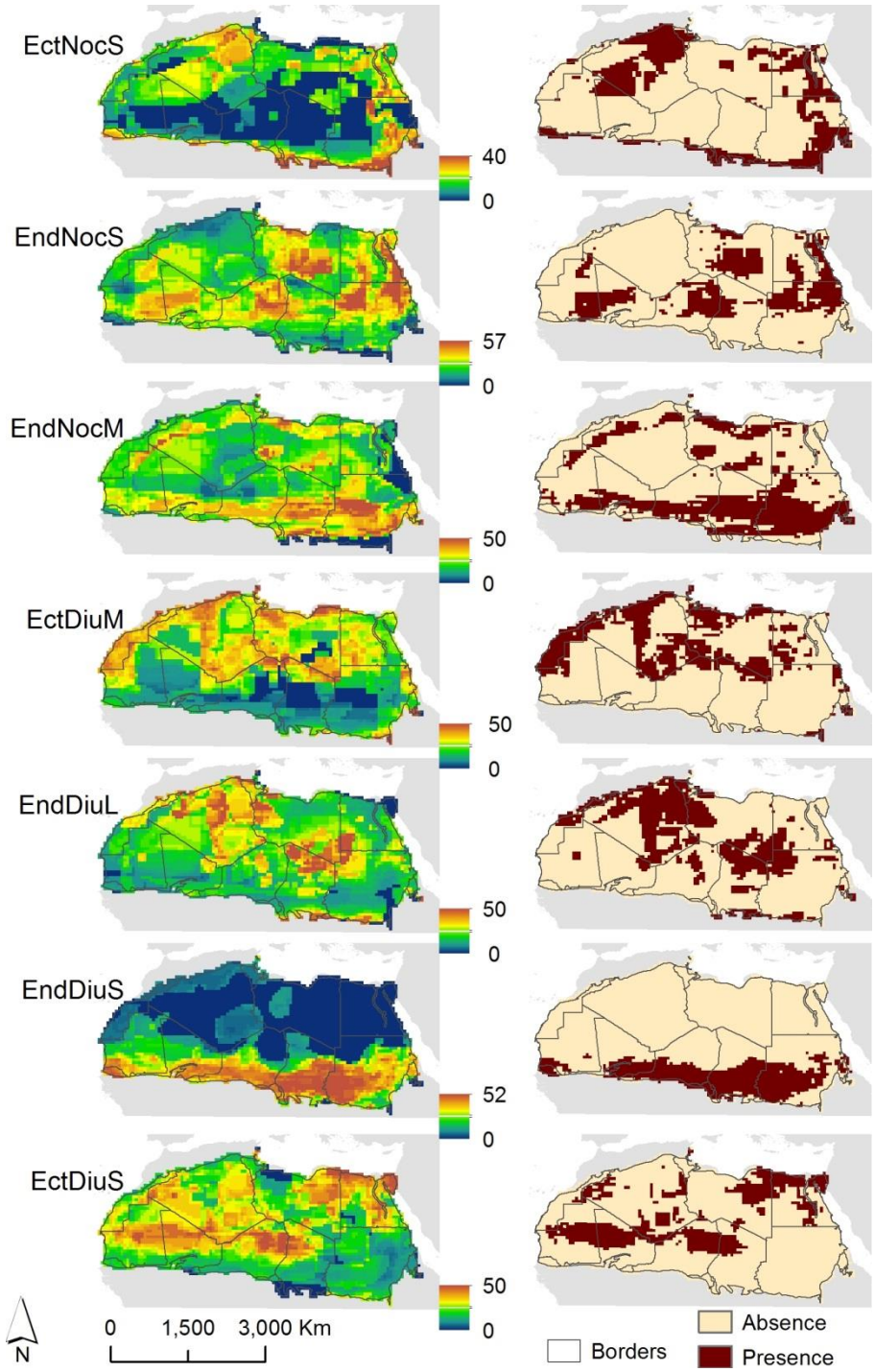

Fig. 6.3 - Distribution patterns of functional groups in the Sahara-Sahel. The left column depicts species richness of each group, expressed as percentage of species of each group in relation to the total number of species per grid cell. The right column depicts the area of occupancy of each functional group.

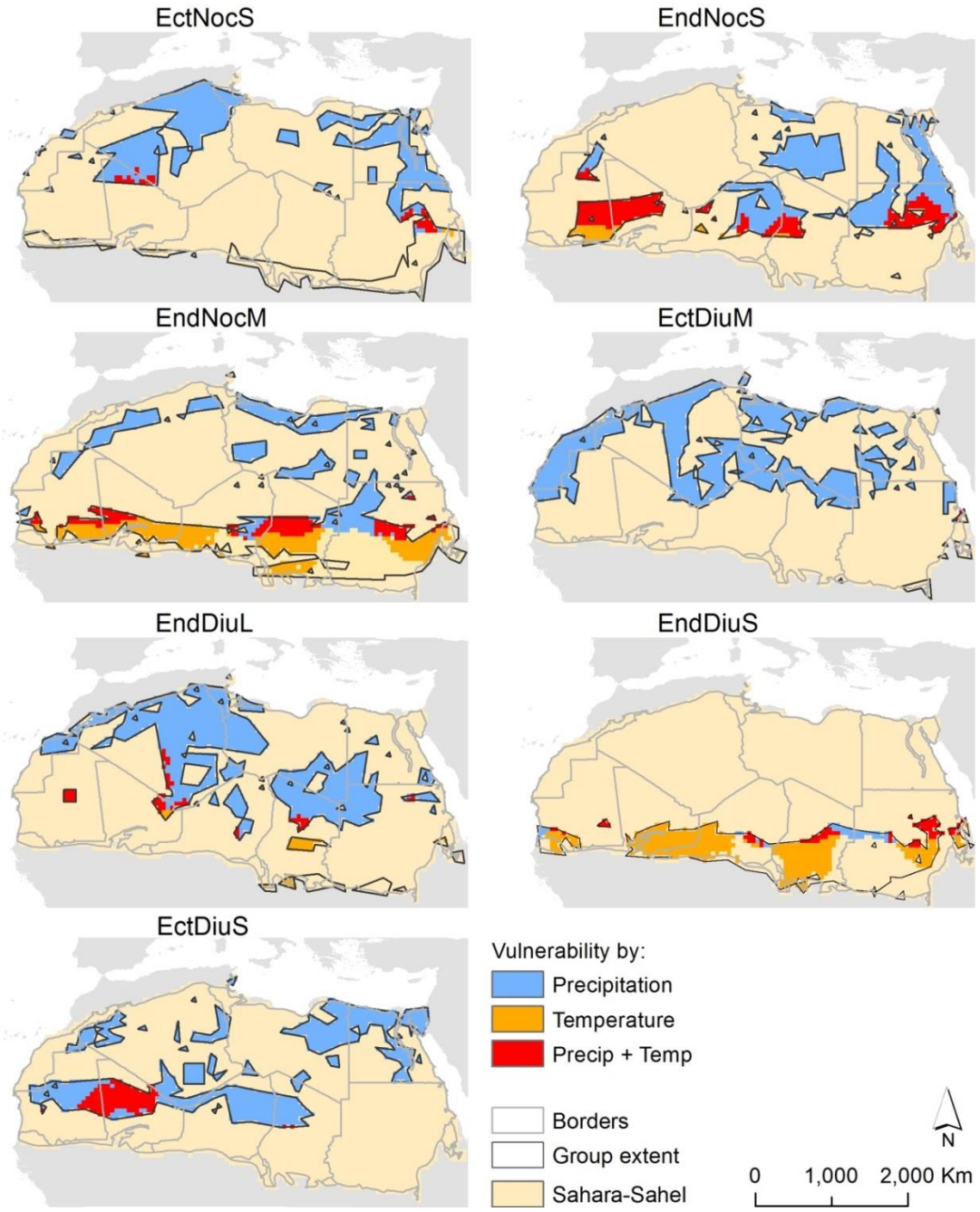

Fig. 6.4- Vulnerability scenarios for each functional group in 2080. Vulnerability identified by magnitude of change in mean annual precipitation (mean of GCM's), in upper annual mean temperature (mean of GCMs + sd), and in both factors (Precip + Temp) by 2080 in comparison to present time. Thresholds to identify vulnerability areas for each functional group were the lower critical temperature (mean of critical temperatures – sd) and 200mm of precipitation. Extent of occurrence of each functional group is presented (black polygons).

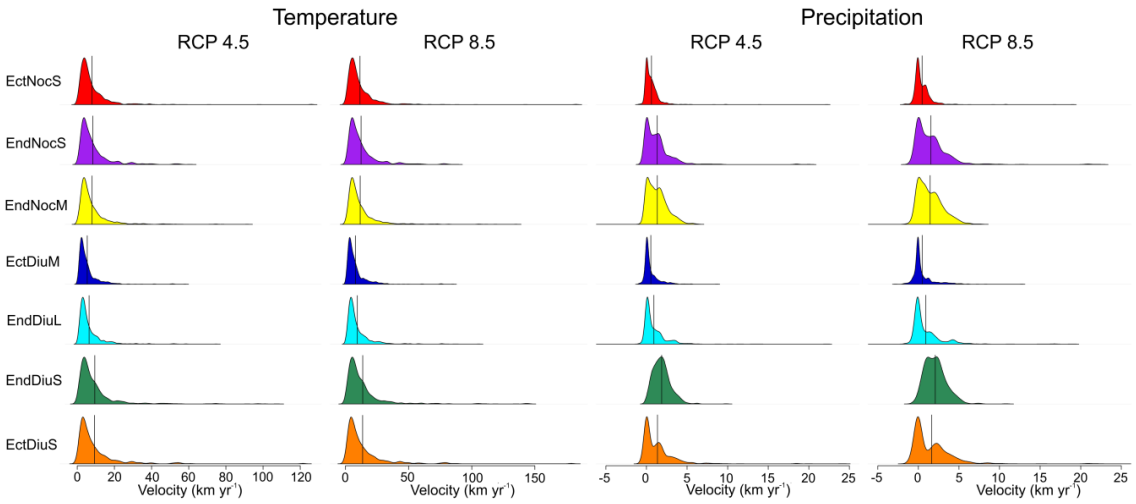

Fig. 6.5 Predicted velocity of climate change within the extent of occurrence of each functional group. Velocity of annual mean temperature (temperature) and annual mean precipitation (precipitation) change calculated for two pathways (RCP 4.5; RCP 8.5). Vertical bars indicate the mean velocity for each group.

DISCUSSION

UNCERTAINTIES IN FUNCTIONAL GROUPS AND CLIMATE CHANGE ANALYSES

Different dimensions of climate change have different implications for biodiversity depending on the degree of a species' exposure, plus its sensitivity to the new conditions and its adaptive capacity to track shifting habitats. We developed a framework for identifying the Sahara-Sahel endemics most vulnerable to the magnitude and velocity of climate change. We did this by measuring their level of exposure and simultaneously using functional groups as proxies for testing sensitivity and adaptive capacities. Despite being challenging, assessments of climate change impacts on biodiversity can benefit from enhanced capacity to represent species by their biological traits (Dawson *et al*., 2011; Araújo *et al*., 2013). Due to the lack of information on species' physiological traits, we recognize the susceptibility of the identified functional groups. The inclusion of quantitative traits (e.g.: water balance, metabolic rate, body temperature, thermal limits, evapo-transpiration, reproduction rates, dispersal capacity) would probably yield more accurate results. To overcome the lack of ecophysiological parameters data, we have increased the number of the biological traits used and have set an upper limited of groups to be created, avoiding a large number of groups characterized by few biological traits.

The Sahara-Sahel region's long-term local conflicts and remoteness hamper biodiversity assessments (Brito *et al*., 2014). As such, there are regional sampling

gaps that cause generalised lack of high resolution observational data (e.g.: GPS points) for the taxa addressed in the current study. Consequently, we based the analyses developed on the extent of occurrence from IUCN, Birdlife and published distribution atlases. Using range polygons forced means we developed analyses with a low spatial resolution (half-degree cells). This hampered the application of ecological niche modelling algorithms for assessing gains and losses of climatically suitable areas. Although range polygons might overestimate areas of exposure, they allow including species with small and narrow ranges for which there is insufficient observational data to derive accurate ecological niche models. The approach here used allows us to analyse the entire species dataset without restrictions.

The low resolution of species distribution data forced climate change analyses to be performed also with coarse spatial resolution. Despite diluting the spatial distribution of climate, uncertainties are more likely to arise from the climate projections used to drive climate models. In fact, GCMs exhibited considerable variation among models, which can affect the accuracy of biodiversity impact assessments under climate change (Buisson *et al*., 2010). Given those variations, we have applied a multi-model ensemble average forecast technique (Loarie *et al*., 2009, Fordham *et al*., 2011). We summarized uncertainty by mapping the upper and lower values of changes in the magnitude of climate change. Yet, to retain the differences among them, we calculated the individual velocity of climate change for each GCMs. Finally, we calculated a mean of the velocity of climate change and its standard deviation of each GCM and pathway, to account for their differences.

We identified the level of exposure of each functional group, by intersecting their range with the distribution of the magnitude and velocity of climate change. We then applied a threshold (minimum critical thermal limit) according to the observed values for endotherms and ectotherms reported in the bibliography (Araújo *et al*., 2013). As we have applied the minimum critical thermal (mean critical temperature – s.d. of the mean critical temperature), the identified areas of exposure to temperature are conservative and probably overestimated. However, we did this because the mean critical thermal limits described in the literature were higher than the expected maximum temperature for the region for 2080 (Araújo *et al*., 2013; IPCC 2013).

FUNCTIONAL GROUPS AND VULNERABILITY TO CLIMATE CHANGE

Functional group and species richness followed similar distribution patterns. The observed strong relation might be due to the extreme environments of the Sahara-Sahel. Species adapted to extreme conditions are likely to converge in physiological

traits due to organism's limitations to adapt to harsh conditions (Bickford *et al*., 2006). As such, areas harbouring more species are expected to present a higher number of functional groups. Yet, this spatial match does not prevent or even preclude assessing the number of functional groups and their vulnerability to the predicted climate changes.

We summarized the functional strategy of the Sahara-Sahel endemics into seven functional groups with different sensitivity and adaptive capacities as well as distribution patterns. Functional groups in the Sahara-Sahel were vulnerable to distinct magnitudes and velocities of climate changes. As expected, they were particularly exposed to changes in precipitation. A lack of precipitation defines deserts (Ward, 2009), so we expect their species to be more vulnerable to precipitation fluctuations, either by the degree of exposure or by sensitivity and adaptive capacities. Both nocturnal and diurnal mammals (EndNocM and EndDiuL, respectively) and birds (EndDiuS) range in areas of decreasing precipitation and/or increasing temperature in the future. Despite being exposed, they might be able to overcome these changes by physiological plasticity. Under extreme temperatures and limited water availability, these species may be able to survive. They present physiological, morphological, and behavioural mechanisms developed to either avoid or tolerate harsh environmental conditions (Holl, 1985; Gouat, 1993, Williams and Tieleman, 2005, Cain III *et al*., 2006; Vale *et al*. 2012). Moreover, they might have the capacity for colonizing other suitable areas. As an example, despite having small home ranges, birds (EndDiuS) exhibit reduced metabolism rates, small clutch sizes, and slow nestling developments (Williams and Tieleman, 2005). As such, they have the capacity to forage food at large distances and/or colonize other suitable areas. Although the combination of sensitivity and adaptive capacity related traits might favour these groups, they include some of the most threatened species inhabiting the Sahara-Sahel (e.g.: *Addax nasomaculatus* and *Nanger dama*). These species have experienced extreme range reductions due to human activities (e.g.: direct persecution, harassment, poaching, and land transformation; Wacher *et al*., 2004). Currently, only around 8.5% of their exposed extent of occurrence is protected. As human's activities might constitute barrier to these species dispersal (Duncan *et al*., 2014), further studies should identify suitable corridors through which species might disperse without human pressure.

The most vulnerable functional groups in the Sahara-Sahel are small mammals and lizards (EndNocS and EctDiuS). They were potentially exposed to changes in the magnitude and velocity of precipitation and also locally exposed to temperature changes. Despite being arid-adapted species, they might be living close to their upper thermal limits. As tolerance to heat is largely conserved across lineages, latter species

will unlikely evolve physiological tolerances to increasing heat (Araújo *et al*., 2013). Lizards (EctDiuS) are directly sensitive to temperature changes due to their thermoregulation mechanisms (e.g. Cowles and Bogert, 1944; Pianka 1970; Hoffmann *et al*., 2013; Ferri-Yáñez and Araújo, 2015). They also have small home ranges and body size and thus low adaptive capacity. Additional, their dispersal is strongly affected by rising temperatures (Massot *et al*., 2008). On the contrary, small mammals (EndNocS) are known to tolerate high body temperatures and/or high environmental temperatures (Boyles *et al*., 2011). They might be able to cope with warming trend, despite overspending energy and potentially compromising the reproduction success and dispersal capacity (Beatley, 1969; Boyles *et al*., 2011). Moreover, the reproduction success and abundance of both groups has still been associated to rainfall and food availability (Beatley, 1969; Pianka, 1970). The level of exposure, associated with a combination of intrinsic and extrinsic traits makes both small mammals and lizards the most vulnerable groups in the Sahara-Sahel. Yet their sensitive and adaptive capacity depends on several of other intrinsic factors such as genetic diversity; phenotypic plasticity, evolutionary rates and life history traits (Dawson *et al*., 2011). In addition, other dimensions of climate change might differently affect these groups. For instance, lizards might be affected by changes in climate extremes, and in distance and direction of change of the analogous climates, due to their low adaptive capacity, particularly low dispersal ability. Further investigation on other dimensions of climate change is needed for the functional groups here identified. Moreover, climate change is more than changes in temperature and rainfall. There are also changes in surface temperature, evaporation and wind, for instance. Further ecological, genetic and physiological studies should be combined to confirm if these groups are able to adapt by ecological plasticity or dispersal to other suitable areas.

VULNERABLE AREAS AND STATUS OF PROTECTION

The flat and arid Sahara-Sahel regions harbour the most vulnerable functional groups. They are predicted to be highly exposed to climate change (Loarie *et al*., 2009). Parts of the ranges of small mammals (EndNocS) and lizards (EctDiuS) were located in the most arid and flat areas of the Sahara-Sahel. These functional groups have been exposed to past climate fluctuations, as the region has experienced multiple dry-wet cycles since the Pliocene (5.3 to 2.5 Mya), which have shaped local biodiversity distribution (Brito *et al*., 2014). While past exposure to climate fluctuations may provide indications on the ability of the functional groups to persist, it is unknown if species will be able to keep pace with future climate changes through behavioural shifts or

dispersal. As a result of ongoing climate warming, it has been observed up-slope movements to higher elevations and latitudes (Parmeson, 2006; Guralnick and Pearson, 2010). During the past climatic oscillations, Sahara-Sahel Mountains were refugia for several species (Trape, 2009; Brito *et al*., 2014). However, their role under future climate changes for most vulnerable functional groups is unknown. Even if mountains hold suitable habitats in the future, the capacity of small mammals and lizards to track rapid climate change is uncertain. At leading-edges, colonization rates are determined jointly by rates of reproduction and dispersal associated with the availability of suitable resources in novel habitats (Angert *et al*., 2011). On the other hand, the vast empty-quarters, where the magnitude and velocities of climate change will be higher, hold some of the most threatened functional groups. Currently, they are crucial refugia for threatened species (e.g.: *Chlamydotis undulate*, *Addax nasomaculatus* and *Acinonyx jubatus*; Saleh *et al*., 2001; Beudels *et al*., 2005; Chammem *et al*., 2012). The location of the threatened function groups and the lack of formerly protection (Table D.3) reinforce their vulnerability to future climate changes. Increasing the size of current protected areas through habitat corridors and the establishment of new reserves has been suggested to try to carry the moving climates and ecosystems (Hannah, 2008; Loarie *et al*., 2009). As both mountains and lowlands are potential refugia in the Sahara-Sahel, a network of protected areas should create connectivity between them. Monitoring programs of biodiversity status and trends should be design to the most threatened species and potentially vulnerable functional groups, as well as to particularly local hotspots, such as small sized mountain inland waters (Vale *et al*., 2015) that may be crucial for local persistence of water-dependent species.

CONCLUSIONS

The combination of different biological traits contributed to the extent to which species are exposed to climate change. Desert-adapted species with low adaptive capacity constituted the most vulnerable functional groups in the Sahara-Sahel. They are also present in other warm deserts in the world, so they might be equally vulnerable to future climatic changes. Indeed, the sensitivity to climate change for desert's tortoises was already observed in the Mojave-Sonora Desert (Barrows, 2011). Our study is a preliminary assessment of the most vulnerable functional groups in the Sahara-Sahel, but further studies should incorporate genetic diversity and evolutionary rates. This study provides indications on level of exposure to climate change and combination of

biological traits related with sensitivity and adaptive capacity that may endanger biodiversity in warm deserts worldwide. The methodological framework here implemented could be applied to other warm deserts as well as to other biomes.

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Chapter 7

General Discussion and Concluding Remarks

"In the end we will conserve only what we love. We will love only what we understand. We will understand only what we are taught"

Baba Dioum

GENERAL DISCUSSION

The main objective of this thesis was to address biodiversity conservation in arid environments, focusing on the Sahara-Sahel where biodiversity is under strong climatic control and is vulnerable to climate change. It intended to contribute to the: i) evaluation of the performance of ecological niche models to predict species distribution at range margins and for ecologically plastic species; ii) the evaluation of the conservation status of mountain restricted species; and iii) the identification of local hotspots of biodiversity and of the functional groups most vulnerable to future climate change. In the first part of this discussion, the key findings are summarized and integrated and their implications for biodiversity conservation are discussed. In the second part, future research is suggested, and the last part of this chapter provides the concluding remarks that could be drawn from this work.

KEY FINDINGS

ECOLOGICAL NICHE MODELS PERFORMANCE

Before this study, it was known that the ecological and biogeographic contexts on which ecological models are developed affected their performance (e.g.: Suárez-Seoane *et al*. 2013), and that global models built with coarser resolutions biased predictions at range margins of species distribution (e.g.: Braunisch *et al*. 2008). Models build for specialist species yielded more accurate than those build for ecologically plastic species with wide geographical ranges (Segurado and Araújo 2004; Buisson *et al*. 2010). Associated, the threshold choice for identifying suitable occurrence areas was known to be an arbitrary decision, mostly dependent of the degree intended for minimizing both commission and omission errors (Liu *et al*. 2005; Jimenez-Valverde and Lobo 2007). After this study, regional models for the Atlantic Sahara-Sahel biogeographic crossroad, using three African widespread species (*Erythrocebus patas*; *Hoplobatrachus occipitalis* and *Procavia capensis*) and one ecologically plastic species *(Papio papio*), built with precise data were identified as being more accurate to predicted current species distribution at species range edges, in comparison to global models, and to define suitable areas for ecologically plastic

species ranging through different biogeographic regions (**ARTICLES I AND II**). The application of conservative thresholds to high resolution regional models also demonstrated to improve model accuracy at species range edges, especially the ones located in abrupt environmental transition zones (**ARTICLE I**).

This work pointed to an overall tendency of global models to overestimate species distribution areas at the range edges or when defining suitable areas for ecologically plastic species (**ARTICLES I AND II**). Yet, their performance can be increased by applying more restricted thresholds (**ARTICLE I**). Notwithstanding, it is important to highlight that global models were able to capture the overall distribution patterns, and that they are still the best option to predict species environment interactions for regions or time periods other than those where models were built (Pearson *et al*. 2002; Thuiller *et al*. 2004; Barbet-Massin *et al*. 2010).

This work emphasized the need for applying **regional models** to predict **current species distribution** at regional scales and informed conservation planning in biogeographic crossroads and for ecologically plastic species. Independently of the threshold selected, high resolution regional models provided more detailed distributions, being in turn more **accurate** and able to discern the most important environmental variables at the edge of species environmental range (**ARTICLE I**) and within different environmental spaces (**ARTICLE II**). High resolution regional models built within an ecologically significant area (e.g. biogeographic regions) were more accurate to set locally oriented priorities for conservation.

Additionally, other important outcomes can be drawn for biodiversity conservation of the Atlantic Sahara-Sahel biogeographic crossroad. The results of the regional models illustrated the *all-or-nothing* character of suitable habitat availability in abrupt environmental transition areas (**ARTICLE I**) and the trend to local niche truncation observed for ecologically plastic species (**ARTICLE II**), supporting the importance of particular microhabitats (e.g. gueltas) to the persistence of Sahara-Sahel biodiversity. The detailed spatial distributions provided by regional models where mostly located in the Atlantic Sahara-Sahel mountains, particularly in the Mauritanian mountains of Adrar Atar, Tagant, Assaba, and Afollé (**ARTICLE I AND II**), emphasizing their importance as island-like mountains important for long-term conservation of biodiversity.

CONSERVATION STATUS EVALUATION

Before this study, the Atlantic Sahara-Sahel mountain endemics *Felovia vae* and *Agama boulengeri* were categorized as Data Deficient and Not Evaluated by IUCN, respectively, due to the lack of knowledge on their local distribution patterns and ecological parameters. After this study, they were both considered Least Concern. Based on predicted suitable maps and species presences, it was calculated the extent of occurrence and area of occupancy for both species. Associated with the number of isolated suitable areas, it was possible to **update the conservation status** of *Felovia vae* (**ARTICLE III**) and to **determine the conservation status** of *Agama boulengeri* (**ARTICLE IV**). All parameters analysed exceeded the thresholds for categorization as Threatened, and both species were deemed Least Concern.

Both species were highly dependent on mountain gueltas. Before this study, gundis were reported to rely on vegetation to regulate their water intake (de Rouffignac *et al*. 1981), but in Mauritanian mountains it became clear that they use direct water sources. *Felovia vae* was observed drinking from gueltas in southern Assaba mountains (see: Figure 4.1.4 **ARTICLE III**). Latter observation emphasized the importance of gueltas as the only source of water for large distances in Mauritanian mountains not only for this species but for other water dependent taxa. As such, the most pervasive threats for both species currently identified are related with future climate change and drought, which may affect water availability in the region.

This study identified **putative barriers to dispersal** for *Felovia vae* and *Agama boulengeri* (**ARTICLES III AND IV**) that may affect population connectivity: i) the dry and dune-covered El Khatt river basin, which probably hampers dispersal between populations located in the Adrar-Atar and in the Tagant-Assaba mountains; and ii) the Karakoro river basin, which probably constitutes a barrier for dispersal between populations located in the Tagant-Assaba and in the Afollé mountain. The latter river basin was also identified as putative barrier for dispersal of *Papio papio* subpopulations in-between southern Mauritanian mountains (**ARTICLE II**). The lower Senegal river valley was also hypothesized as probable barrier for dispersal (**ARTICLES II, III AND IV**), probably due to the lack of significant rock outcrops that are required by *Felovia vae* and *Agama boulengeri*, and the abundance of agriculture fields and human activities that may be related to the absence of *Papio papio* populations. The putative barriers to dispersal identified in-between Atlantic Sahara-Sahel mountains by this study need further testing with local ecological studies and molecular markers, to confirm if they constitute barriers to gene-flow.

LOCAL HOTSPOTS OF BIODIVERSITY

Presently, most conservation efforts target the global biodiversity hotspots as they are areas of exceptional endemic richness that are undergoing significant habitat loss. After this study, mountain rock pools (gueltas) were recognized as local biodiversity hotspots, also deserving global attention.

Identifying priority areas for biodiversity is essential for directing conservation resources (Jenkins *et al*. 2013). As such, most conservation organizations allocate funds to areas that have been identified as priorities for global conservation investment, such as the **biodiversity hotspots** (Dalton 2000; Brooks *et al.* 2006; Halpern *et al.* 2006). Such approach may miss regional patterns and small-sized areas with large number of endemics under threatened. Conceptually, the global identification of priority areas have been all fit within the framework of ‘‘irreplaceability’’ relative to ‘‘vulnerability’’ (Margules and Pressey 2000). The application of this framework to the Mauritanian mountains allowed identifying gueltas as **local hotspots of biodiversity**. They gathered a large proportion of the country endemics and they are simultaneously threatened by drought and human pressure, in an area representing only 0.00004% of the country. This makes gueltas special places, disproportionately important for their tiny size, deserving global attention as well (**ARTICLE V**).

Gathered information clearly pointed gueltas as local biodiversity hotspots, but also showed their importance for local human communities (**ARTICLE V**). The Sahara-Sahel covers several countries of low economical income and low human development (UNDP, 2010), where livestock plays an important economic role. Communities of agriculturalists and herdsmen base their activities in the exploration of the water and surrounding habitats of gueltas leading to activities of excavating pools and pumping water and to fecal contamination of water. Although local beliefs protect mountain-ranging crocodiles (Brito et al 2011), increasing human activities since the 1970’s droughts are pressuring local biodiversity. Water is the main driver of species diversity and human occurrence in gueltas. In fact, these water-bodies may be the only source of water for large distances. Hence, conservation plans to protect them need to incorporate sustainable water management as fundamental resource.

INTEGRATIVE PATTERNS ON BIODIVERSITY DISTRIBUTION

This study provided multiple evidences for a generalized biodiversity distribution pattern in the Atlantic Sahara-Sahel: **species diversity is most related with availability of gueltas**. This distribution pattern was consistent in a large proportion of vertebrate species analyzed (**ARTICLES V**), as well as in other species analyzed with further detail, including *Procavia capensis*, *Papio papio*, *Felovia vae*, and *Agama boulengeri* (**ARTICLES I, II, III AND IV**). In these four case-studies, species occurrence was related to presence of gueltas, and in Mauritania they were restricted to mountain populations that may be isolated, putatively by the same geographical barriers to dispersal. The emerging pattern in this study emphasized the importance of Mauritanian mountains as island-like mountains, and gueltas as local hotspots of biodiversity that may provide possible refugia under future climate change.

The observed value of gueltas can probably be extrapolated to the remaining gueltas of the Sahara-Sahel (Fig. 6.1). The Sahara-Sahel past climatic oscillations has greatly shape biodiversity distribution. During wetter periods, the Afro-tropical ecoregion has expanded throughout the current Sahara-Sahel while in the dry periods it was restricted to mountains refugia (Brito *et al*. 2014). Due to the current aridity increase phase, the Atlantic Sahara-Sahel mountains, particularly in Mauritania, act as refugia for relict populations of Mediterranean and Afro-tropical species (**ARTICLE II**) and endemic species (**ARTICLES III AND IV**). This pattern is observed elsewhere in other mountain of the central and eastern Sahara-Sahel (Anthelme *et al*., 2008; 2011). Furthermore, gueltas within mountains are being described as potential micro-refugia, acting as speciation drivers (Brito *et al*. 2014). In fact, aquatic ecosystems are evolutionary and ecological refuges in arid environment, and they might constitute future refuges under global and regional climatic changes (Davis *et al*. 2013). Due to the warming trends, it is likely that Sahara-Sahel gueltas will also constitute refugia under future climate change, particularly for water-dependent species.

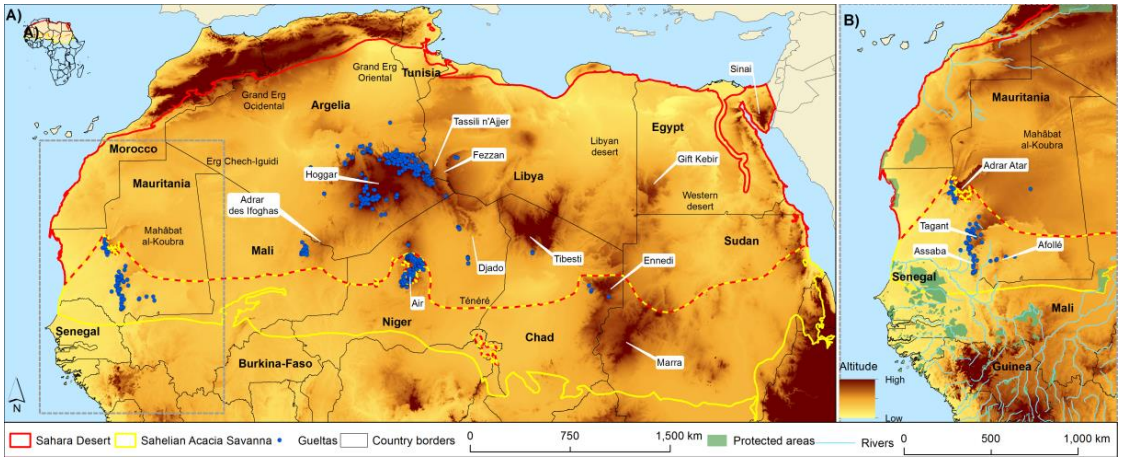

Fig. 7.1 - (A) Distribution of rock pools (gueltas) in the Sahara-Sahel (adapted from Brito *et al.* 2014). Gueltas are mostly concentrated in mountains. (B) Distribution of gueltas in Mauritania mountains (adapted from Vale *et al*. 2015).

SAHARA-SAHEL FUNCTIONAL GROUPS AND VULNERABILITY TO FUTURE CLIMATE CHANGE

Presently, assessments of potential climate change impacts have been mostly focused on predicted changes in species distribution (Foden *et al.* 2013). These assessments may fail in reflecting the intrinsic responses of species to climate change, which is mostly mediated by physiological, ecological and evolutionary traits (Dawson *et al*. 2011; Foden *et al.* 2013). The evolutionary history, the physiological plasticity, and the acclimation potential (thermal compensation via physiological adjustment of an organism) are factors known to increase species resilience to climate change (Seebacher *et al.* 2014). Species living in areas subjected to frequent and extreme climatic fluctuations, like in the Sahara-Sahel, are likely to have more adaptive capacity or phenotypic plasticity under climate changes. After this study, the functional strategy of each Sahara-Sahel endemics was summarized, and **seven functional groups with different sensitivities and adaptive capacities**, and different levels of vulnerability to climate change, were identified. Generally, functional groups were **more vulnerable to changes in the magnitude and velocity of precipitation** in comparison to temperature changes. The most vulnerable functional groups were distributed mostly in flat areas, and constituted by species simultaneously sensitive and with low adaptive capacity.

In this work, two desert-adapted functional groups (comprising diurnal ectotherms and endotherms with low adaptive capacity) were identified as the most vulnerable groups to future climate change, mostly due to their low adaptive capacity (dispersal abilities)

but also sensitivity (**ARTICLE VI**). Although, dryland biodiversity is clearly adapted to climate extremes and variations, the rate of future climate change may be too fast for some species to adapt, especially the ones living closely to their climatic threshold for survival (Davies *et al.* 2012). Other desert-adapted functional groups were suggested to be able to persist under future climate change (comprising desert ungulates and gundis), due to their high dispersal capacity associated with desert adapted mechanism of thermoregulation and/ or morphological adaptations to dry conditions (**ARTICLE VI**). However, some are presently vulnerable due to human persecution (uncontrolled hunting and poaching). Thus, even if they are able to keep pace with future climate change, they might be limited by their small population size and by human pressures. This work suggested that, contrarily to expected, desert-adapted Sahara-Sahel functional groups combined ecophysiological traits and biogeographical conditions that make them the ones most vulnerable to climate change, indirectly or indirectly.

Potential impacts of climate change on the Atlantic Sahara-Sahel biodiversity have also been identified for the mountain-restricted northernmost populations of *Papio papio* and the endemics *Felovia vae* and *Agama boulengeri*. Vulnerability was associated to the local strong dependency on gueltas and water availability (**ARTICLES II; III AND IV**). As such, drought and extreme temperatures were identified as the major threats affecting all gueltas and their biodiversity (**ARTICLE V**). Distinct combinations of **physiological and evolutionary traits** related with species adaptive and dispersal capacities determine the extent to which they vulnerable to future environmental changes. Further research on such parameters is needed.

Climate change is considered to be an important driver of ecological shifts in the world's arid and semi-arid regions (Davies *et al.* 2012). It is likely to severely impact drylands, and in combination with the habitat loss and fragmentation, it will reduce opportunities for arid-adapted biodiversity to adjust, or keep pace and physically move to more suitable habitats as climate zones shift. The functional characteristics of the groups identified in Sahara-Sahel as the most vulnerable under climate change may probably be representative of other warm deserts. Similar combinations of ecophysiological and biogeographical traits may be found in species inhabiting similar environmental pressures. As such, patterns here described may very well apply to other global warm deserts, but further testing is needed.

FUTURE PROSPECTS

This work contributed to increase the general understanding of Sahara-Sahel biodiversity distribution patterns, especially in the Atlantic Sahara-Sahel biogeographic crossroad, laying the foundations to build an effective conservation plan for the region. Still, there are knowledge gaps in biodiversity patterns and processes and their relations with local human communities. The future challenge is to increase comprehension on patterns of species diversity, distribution and ecology, and to understand the evolutionary processes linked to such diversity, in order to systematize biodiversity conservation planning. As such, several questions need to be answered in order to design cost-effective conservation planning.

In the Atlantic Sahara-Sahel, further field sampling is needed to fill distribution gaps. Despite fieldwork developed in the last years (Brito *et al*. 2014), there are still gaps in areas like the extreme southern Morocco and the northern and eastern provinces of Mauritania. Additionally, further analysis using ecological niche models based on high-resolution observations should be performed throughout the Sahara-Sahel, to derive comprehensive and integrative patterns about relationships between environmental variation and biodiversity distribution and to map biodiversity distribution. Atlases of species distribution in the Atlantic Sahara-Sahel are still missing at all taxonomic levels and are basal for biodiversity conservation planning.

The conservation status of about 37% and 4% of Mauritanian vertebrates is assigned as Data Deficient or Not Evaluated respectively. The definition of species conservation status is one of the first steps for biodiversity conservation (Butchart *et al*. 2006). The application of ecological niche models, developed in this study to identify suitable areas for species occurrence and quantify isolated populations, should be expanded to other poorly known taxa to update or evaluate their conservation status.

This study demonstrates the importance of Sahara-Sahel mountains as local biodiversity refugia, and emphasizes the importance of their gueltas as local hotspots. This study provides basal data to protect these local hotspots of biodiversity, yet further ecological and genetic assessments are still needed for quantifying biodiversity levels. Cryptic diversity has been observed in multiple taxa (Gonçalves *et al*. 2012; Dilyte 2014; Kapli *et al*. 2015; Metallinou *et al*. 2015).The taxonomy and systematics of many species is still uncertain, and molecular tools should be applied to identify taxonomic units, endemic species and/or clades and most important, identify Evolutionarily Significant Units (ESUs) for conservation.

This study assessed species level status diversity in mountain gueltas, but additional field sampling is needed to quantify species abundance and population trends in each guelta. Also, biodiversity assessments should be extended to other taxonomic groups beyond those assessed in this thesis, such as aquatic flora, aquatic macro-invertebrates, birds and bats, which are often allied with water-bodies in deserts and arid regions. As an example, aquatic macro invertebrates are considered good indicators of water quality in arid environments (McBurnie *et al.* 2014), thus their identification could also contribute to manage potential disease-vector species in gueltas and further contribute to improve public health.

Local drivers of biodiversity distribution in mountains gueltas are still poorly understood. This study identified primary productivity and size-related traits of gueltas as most related with species diversity, but additional information is needed on other likely relevant topographic, environmental and ecological characteristics. These include: i) physicochemical parameters, such as temperature, pH, conductivity, dissolved oxygen and turbidity; ii) nitrates and nitrites concentrations; iii) organic suspend matter; and iv) concentration of chlorophyll a, which is a proxy for algal biomass. Such estimations would allow quantifying water quality parameters also related to public health and to set quality monitoring programs. Moreover, these physicochemical parameters could give indication on local systems resilience to fecal contamination and eutrophication.

This study identified human-water and human-biodiversity conflicts, suggesting that conservation plans to protect gueltas should include the economic benefits that local communities can derive from ecosystem services. These include sustainable use of water, ecotourism, and public health. For instance, organized ecotourism programs may be considered for accessible gueltas for observation of crocodiles and other relict fauna and flora. Local awareness campaigns focusing on the biodiversity value of gueltas should be promoted to inform local communities. Analyses based on return-on investment (ROI) frameworks are needed to evaluate the viability of distinct local management plans. Reserve selection algorithms accounting with species, functional and phylogenetic diversity, as well as socio-economic factors and costs (within a ROI framework) could be developed to identify targets for cost-effective priority areas for conservation.

In this study, functional groups vulnerable to climate change were identified based in surrogate traits, given that detailed ecophysiological parameters related to potential taxa adaptation to climate change are unknown. Quantifying ecophysiological data (including geographic variation) on species thermal physiological tolerances, reproduction rates, generation time, body temperatures, and local abundances would

be valuable to evaluate probability of persistence under climate change. Such task is clearly highly demanding, and will require concerted efforts between multiple research teams.

The designing of management options in face of local biodiversity conservation and human development requires strong organizations and communities with the skills, knowledge and data to undertake a broad range of technical and process-based activities. Presently, Mauritania displays a deficit on equipment and qualified human resources to perform biodiversity assessments using contemporary tools (molecular and spatial data). Local capacity building, targeting joint collaborative biodiversity research and advanced training of human resources, is urgently needed.

CONCLUDING REMARKS

This study integrated species distribution data and functional data on Sahara-Sahel biodiversity, which allowed evaluating the performance of ecological niche models, mapping biodiversity at specific and functional levels, identifying distribution patters in individual species and functional groups, and evaluating vulnerabilities to climate change. The assembled knowledge has allowed improving ecological niche models accuracy for range margins populations and for ecologically plastic species, updating and evaluating species conservation status, identifying local biodiversity hotspots and priorities for conservation, and identifying and mapping functional groups vulnerable to predicted magnitudes and velocities of climate change. Furthermore, this study contributed to increase the available knowledge on biodiversity distribution patterns in deserts and provided recommendations for future conservation actions. The major conclusions of this work are:

1. Regional models with precise data are more accurate to predicted current species distribution at range margins locate in biogeographic crossroads and in defining suitable occurrence areas for ecologically plastic species ranging throughout distinct biogeographic regions. Conservative thresholds applied to high resolution regional models improve model accuracy in range edges, especially when they are located in abrupt environmental transition zones.

2. For local conservation planning, and especially to identify optimal surveys sites under present conditions, fine resolution regional models should be applied instead of models built with coarse resolution data. In absence of high

resolution data, downscaled models within the same area extent are valuable options.

3. For ecologically plastic species ranging throughout distinct biogeographic regions, regional models are the most accurate in distinguish local environmental predictors and suitable areas of occurrence. Regional models may be the most cost-effective option for defining accurate ranges and for effectively designing protected areas for ecologically plastic species.

4. The mountain endemics of the Atlantic Sahara-Sahel, *Felovia vae* and *Agama boulengeri*, were both mostly related with rock-pools, rocky deserts and bare areas, and were mostly associated to Mauritanian mountains, being likely susceptible to climate change. They were classified as Least Concern following IUCN criteria.

5. Gueltas are tiny places that hold high number of species, including endemics, and they are vulnerable to droughts and human activities. They are local hotspots deserving global attention.

6. The mountains of the Sahara-Sahel and their gueltas have high biological value. Mountains and associated gueltas are currently evolutionary and ecological refugia for several species, and they might continue to provide refugia under future climate change. They are crucial for long-term conservation of Sahara-Sahel biodiversity.

7. Gueltas are crucial for biodiversity conservation and also for local human communities whose economy is based on water exploitation from gueltas and surrounding productive habitats. Future conservation plans should enhance biodiversity conservation while promoting as well sustainable water management in Sahara-Sahel mountains.

8. Seven functional groups with different sensitivity and adaptive capacities were identified in the Sahara-Sahel. Groups were distinctly threatened by specific magnitudes and velocities of temperature and precipitation changes according to their current range. Most of the groups were more exposed and vulnerable to the magnitude and velocity of the precipitation change than to temperature changes.

9. The more vulnerable functional groups were distributed mostly in flat areas, where predicted magnitude and velocities of change were also the highest. They were constituted by arid-adapted species, but sensitive and with low adaptive capacities. The identification of vulnerable functional groups in the Sahara-Sahel provides indications on vulnerability to climate change in other warm deserts of the world.

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Appendix A - Ecological niche models performance at range margins

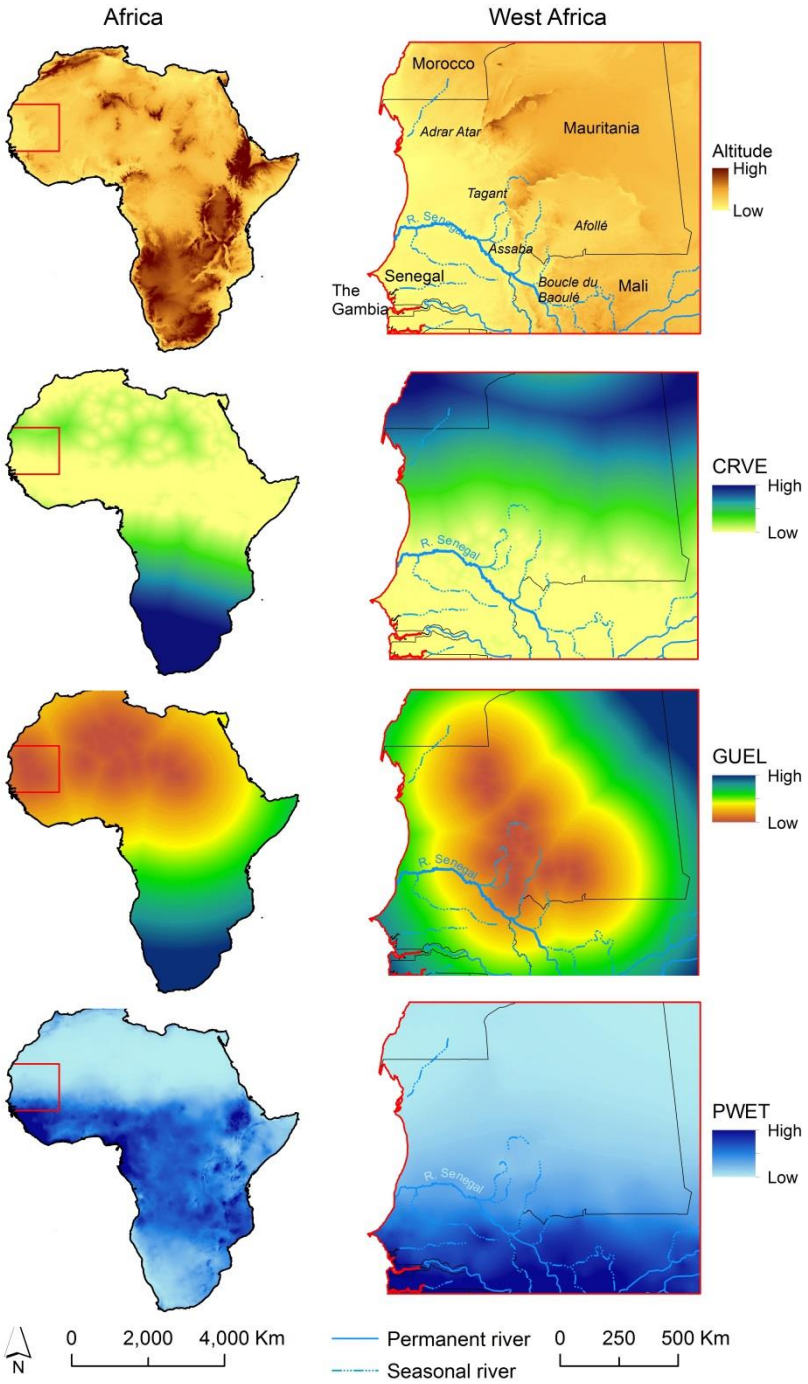

Fig. A.1 - Spatial variation in altitude, distance to mosaics of cropland/vegetation (CRVE), distance to rock pools, gueltas (GUEL) and annual average total precipitation of wettest month (PWET) in Africa and West Africa. West Africa study area in Africa context and West Africa main features and toponomies.

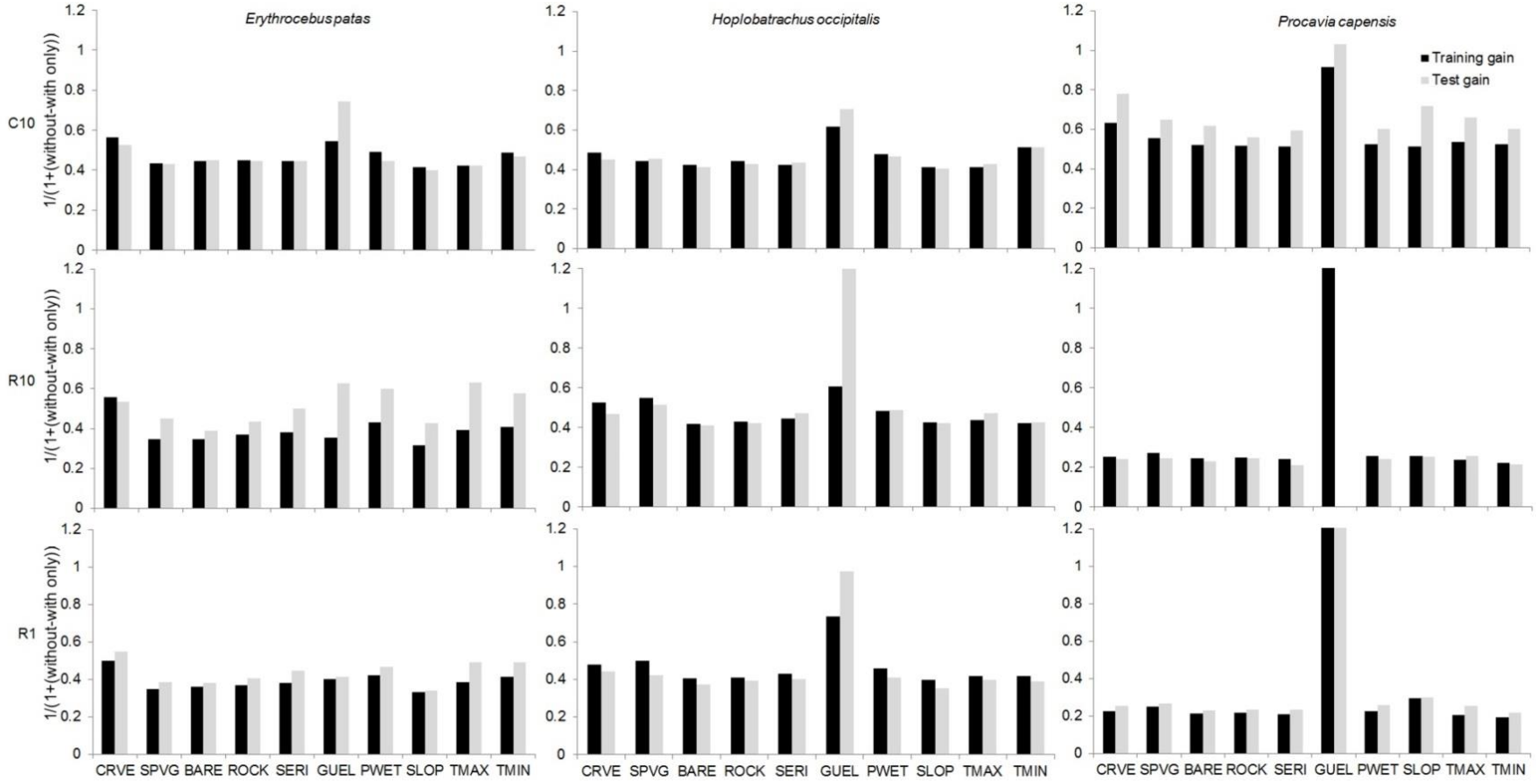

Fig. A. 2 - Jackknife results for the environmental factors used in each maximum entropy model type for the target species. For each variable, the differences in average gain between models built without a given variable and models built with only that variable using training and test data are presented. Variables with higher differences are the ones most related to species distribution. Explanation of variable codes is given in Table 3.1.

List A.1: *Bibliographic references from where observations were collected*

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METHODS A.1:

TARGET SPECIES

As model systems, we studied three widespread African vertebrates that in West Africa occur in peripheral and isolated populations (Fig. 3.1): 1) the Patas monkey (*Erythrocebus patas* Schreber, 1774) ranges from north of the equatorial forests to the southern limit of the Sahara, and from western Senegal to central Ethiopia, where it occupies plains from open grassland to wooded savannas and dry woodlands. Marginal populations are found in Mauritanian mountains, and Aïr (Niger) and Ennedi (Chad) mountains in the Central Sahara, where the species is restricted to productive environments around rocky pools (locally known as *gueltas*), rivers and streams (de Jong *et al*. 2009; Brito *et al*. 2010); 2) the Bull frog (*Hoplobatrachus occipitalis* Günther, 1858) is a savannah species ranging from southern Mauritania to Ethiopia, through East Africa to northern Zambia, occupying many habitats and associated with small to medium-sized temporary bodies of water. Marginal populations are found in south-western Libya, in Mauritanian mountains, in the Aïr mountains, and in Adrar des Iforas (Mali), where it is restricted to *gueltas* and other temporary water features (Rödel *et al*. 2006; Padial *et al*. in press) 3) the Rock hyrax (*Procavia capensis* Pallas, 1766) is distributed throughout sub-Saharan, north-east Africa, and west Arabian Peninsula, occupying a wide range of habitats, from arid deserts to rainforest, but typically associated with rocky outcrops, cliffs or boulders. Isolated populations are found in Mauritanian and Algerian mountains, where it appears to be dependent of permanent water sources (Barry *et al*. 2008; Brito *et al*. 2010) (Fig. 3.1).

TRAINING AREAS

The West Africa training area is located in a biogeographic transition between Palaearctic and Afro-tropical regions, where the southern range limit of species with Palearctic affinity meets with the northern range limit of species with Afro-tropical affinity (Dekeyser and Villiers 1956; Barry *et al*. 1987; Brito *et al*. 2010; Isenmann *et al*. 2010). There is a cool, dry season from November to February and a hot, dry season from March to June (Cooper *et al*. 2006). Annual average temperature ranges from 20.4 ºC in coastal Southern Morocco to 30.8 ºC in Western Mauritania (Hijmans *et al*. 2005). There is a marked north-south gradient in annual precipitation, from 11 mm in the north-eastern desert areas to 1334 mm in the extreme southern region (Hijmans *et al*. 2005). Rain falls in a single wet season from July to October, with most precipitation in August and September (Cooper *et al*. 2006). Most of the study area is covered by sandy, stony and bare deserts (30.0%, 17.9%, 10.0%, respectively; Bicheron *et al*. 2008), but croplands and mosaics cropland/vegetation (17.6%), and close to open shrublands and grasslands (11.8%) are more frequent in southern regions. The region is characterised by a latitudinal gradient in climate and habitat (Anyamba &Tucker 2005). This gradient is disrupted by mountains, which are characterised by a mix of both Mediterranean and Tropical climates (Le Houérou 1997) and provide suitable habitats for otherwise absent widespread African species.

SPECIES DATA

For Africa dataset, observations were randomly selected from a cluster of species occurrences and two datasets were built: 214 observations for training and testing and another with 134 observations for validating models (Table A.1). In both training and validation datasets, clustering of observations was decreased by randomly removing localities that were clustered according to the Nearest Neighbour Index (NNI) given by ArcGIS 9.3: 0.88 (p=0.07) and 0.83 (p=0.08) in *E. patas*, 0.92 (p=0.15) and 0.88 (p=0.05) in *H. occipitalis*, and 0.88 (p=0.06) and 0.82 (p=0.05) in *P. capensis* for the training and validation datasets, respectively.

We followed the same methodology for West African data. Observations were randomly selected from a cluster of species occurrences and two datasets were built: 101 observations for training models and another with 41 for validating models (Table A.1). The clustering of observations was decreased in both datasets by randomly removing clustered localities, according to NNI: 0.91 (p=0.29) and 2.70 (p=0.00) for *E. patas*, 0.92 (p=0.32) and 0.88 (p=0.26) for *H. occipitallis*, and 0.86 (p=0.22) and 1.75 (p=0.00) for *P. capensis* for training and validation datasets, respectively.

To quantify prediction biases in ENMs, we randomly generated a pseudo-absence dataset, with the same number of observations used in the training datasets. Pseudo-absences (hereafter absences) likely corresponded with true absences because they were selected from areas outside buffers encompassing the IUCN polygons of species distribution (IUCN, 2011) and the presence dataset of each species. The buffer sizes were set according to study areas: 1) 100km around IUCN polygons of species distribution for Africa; and 2) 10km around the observations of *H. occipitalis* and *P. capensis* and 40km around *E. patas* observations in West Africa. Buffer size in West Africa was set according to home range size estimations, which were larger for *E. patas* (Isbell & Chism, 2007).

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METHODS A.2:

MODELLING STRATEGY
ECOLOGICAL-NICHE FACTOR ANALYSIS

To quantify parameters related to niche breadth of each species and to identify EGVs related to species distribution in the continental and regional training areas, we performed an Ecological-Niche Factor Analysis (hereafter ENFA), using the Biomapper 4.0 software (Hirzel *et al*. 2004). ENFA compares the distributions of the EGVs values between the species occurrence data set and the whole study area and summarises all EGVs into new uncorrelated factors with ecological meaning (Hirzel *et al*. 2002). The first factor explains species marginality and describes how far the species optimum is from the mean habitat in the study area, i.e. the direction in which the species' niche differs most from the available conditions in the study area (Hirzel *et al*. 2002). The coefficients of the scores matrix related to the marginality factor (MF) indicated the correlation between each EGV and the factor. It ranges from 0 in species living in average habitat conditions to 1 in species far from their habitat average, such as living in extreme habitats. The other factors explain the specialisation, which represents the magnitude of the species niche compared with the available habitat, varying between 1 in generalist species, and infinite in specialist species. Given that specialisation measures are not directly comparable (lack of an upper limit), we used the inverse of

specialisation, tolerance (TS), which varies from 0 for species with a narrow niche, to 1 for species with a wide niche (Hirzel *et al*. 2002).

To perform ENFA, we first converted the two presence data sets of the target species (Africa and West Africa data sets) and the EGVs into Idrisi-formatted maps. Initially, we performed a covariance matrix to check EGVs variability and then developed three models for each species using distinct training areas and pixel sizes: C10, R10, and R1. To determine the importance of each EGV for explaining the distribution of the species, we checked first factors of the score matrix of each model. We extracted the niche breadth parameters, marginality (MF) and tolerance (TS), from each ENFA output.

MAXIMUM ENTROPY APPROACH

We derived models of species probability of occurrence in both training areas, using Maxent (Phillips *et al*., 2006). Together with the background data, this technique requires only presence data as input and consistently performed well in comparison to other methods (Elith *et al*., 2006; Hernandez *et al*., 2006). The background data is a sample of the distribution of the environmental variables in each training area. We developed three models for each species using distinct training areas and pixel sizes: C10, R10, and R1. 10 model replicates were built for each model type with random seed. Observations for each replicate were chosen by bootstrap allowing sampling with replacement in each model replicate. Observations were randomly chosen as test data (10%) for each model. We ran models with auto-features and logistic output (Phillips *et al*. 2006). We took the average area under the curve (AUC) of the receiver-operating characteristic (ROC) plot as a measure of model fitness (Fielding and Bell 1997). The 10 replicates were averaged to generate a forecast of species presence probability, which is a robust procedure to derive consensus predictions of species likelihood of presence (Marmion *et al*. 2009).

We determined the EGVs' importance for explaining species' distribution from their average percentage of contribution and permutation importance to each training model, and their average gain with training and test data using a Jackknife analysis. We determined the relationship between species' occurrence and EGVs by visual examination of response curves profiles from univariate models. Finally, we projected the coarse scale regional and continental models to the fine scale at the regional extent.

EVALUATION OF MODEL PERFORMANCE

To evaluate model performance for identifying suitable areas for species occurrence, we reclassified the three training models (C10; R10 and R1), the two projections (pC10 and pR10), and the West Africa extraction (cC10) to display areas of probable presence or absence for each species, using three different threshold values for species presence. Given that threshold choices should be adjusted to the prevalence of the training data (Lobo *et al*., 2008), we selected the minimum training presence threshold (MTP) and the tenth percentile training presence threshold (10%TP) which rely only on presence data, and the maximum training sensitivity plus specificity threshold (MaxSS) which accounts both presence and absences data: 1) the MTP forces all training observations to be considered as predicted. To calculate MTP for each species in each model, training observations were intersected with the average probability of occurrence models and the minimum probability value was taken as the MTP; 2) the 10%TP assumes that tenth percentile of presence data may have identification errors and/or lack of resolution (Raes *et al*., 2009). To calculate 10%TP, we used the same approach used for MTP, but the minimum probability for 90% of the observations was taken as the 10%TP; and 3) MaxSS minimises both omission and commission errors (Liu *et al*., 2005). To calculate the MaxSS for each species and model types, both the model training observations and the absence datasets were intersected with the average probability of occurrence model. The point of intersection of both training observations and absences curves was taken as the MaxSS. Thresholds were then used to classify average continuous probabilities into binary maps for all areas and projections.

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Table A.1 - Number of observations of each target species used to train (N Train), test (N Test), and validate (N Valid) three maximum entropy model types, and average and standard deviation of training and test AUC of each model. Models were continental at 10x10km (C10), regional at 1x10km (R10), and regional at 1x1km (R1).

Models	Ntrain	NTest	N Valid	AUC (SD)	Test AUC (SD)
Erythrocebus patas					
C10	57	6	30	0.94 (0.04)	0.90 (0.03)
R10	31	3	5	0.97 (0.05)	0.92 (0.06)
R1	31	3	5	0.97 (0.04)	0.93 (0.06)
Hoplobatrachus occipitalis					
C10	75	8	67	0.94 (0.04)	0.91 (0.04)
R10	41	4	27	0.95 (0.05)	0.88 (0.11)
R1	41	4	27	0.95 (0.05)	0.90 (0.05)
Procavia capensis					
C10	62	6	37	0.89 (0.09)	0.79 (0.08)
R10	20	2	9	0.99 (0.00)	0.99 (0.01)
R1	20	2	9	1.00 (0.00)	0.99 (0.00)

Table A.2 - Matrix of the correlation coefficients in the training areas (Africa and West) and scales (1x1km and 10x10km).

Africa	CRVE	SPVG	BARE	ROCK	SERI	GUEL	TMIN	TMAX	SLOP	PWET
CRVE	1									
SPVG	-0.12	1								
BARE	0.24	0.40	1							
ROCK	0.05	0.66	0.69	1						
SERI	0.23	0.51	0.77	0.73	1					
GUEL	0.86	-0.04	0.34	0.22	0.35	1				
TMIN	-0.42	0.39	0.24	0.47	0.28	-0.16	1			
TMAX	-0.44	-0.20	-0.47	-0.47	-0.44	-0.68	-0.04	1		
SLOP	0.06	-0.03	0.07	0.05	0.06	0.15	-0.07	-0.33	1	
PWET	-0.01	0.49	0.46	0.74	0.48	0.21	0.55	-0.47	0.14	1

West Africa (10x10km)										
CRVE	1									
SPVG	0.65	1								
BARE	-0.16	0.18	1							
ROCK	-0.46	0.06	0.53	1						
SERI	0.59	0.71	0.13	-0.19	1					
GUEL	0.33	0.57	0.19	0.17	0.56	1				
TMIN	-0.78	-0.64	0.07	0.36	-0.61	-0.5	1			
TMAX	0.26	0.49	0.11	-0.17	0.66	0.19	-0.44	1		
SLOP	-0.11	-0.09	-0.04	0.16	-0.12	-0.13	0.09	-0.05	1	
PWET	-0.75	-0.34	0.27	0.81	-0.47	0.06	0.56	-0.35	0.16	1

West Africa (1x1km)										
CRVE	1									
SPVG	0.65	1								
BARE	-0.16	0.18	1							
ROCK	-0.46	0.06	0.53	1						
SERI	0.59	0.71	0.14	-0.19	1					
GUEL	0.33	0.57	0.19	0.17	0.56	1				
TMIN	-0.78	-0.64	0.07	0.36	-0.61	-0.5	1			
TMAX	0.26	0.49	0.11	-0.17	0.66	0.19	-0.43	1		
SLOP	-0.11	-0.09	-0.05	0.15	-0.12	-0.13	0.09	-0.04	1	
PWET	-0.75	-0.34	0.26	0.80	-0.47	0.06	0.56	-0.35	0.15	1

Table A.3 - Measures of predictive accuracy calculated from a 2 × 2 error matrix. Sensitivity is the probability that the model will correctly classify a presence. Specificity is the probability that the model will correctly classify an absence. The kappa statistic (Kappa) and the True Skill Statistic (TSS) normalize the overall accuracy by the accuracy that might have occurred by chance alone. All measures were calculated for all the maximum entropy model types of the target species and three thresholds: minimum training presences (MTP), 10th percentile training presence (10%TP), and maximum training sensitivity plus specificity (MaxSS). All measures are given for models: continental at 10x10km (C10), regional at 10x10km and at 1x1km (R10 and R1, respectively), for projections C10 into West Africa at 1x1km (pC10) and R10 into West Africa at 1x1km (pR10), and for the West Africa extraction (C10 Clip) from the C10.

Threshold	Measures	C10	cC10	pC10	R10	pR10	R1
		Erythrocebus patas					
MTP	Sensitivity	1.00	1.00	1.00	1.00	1.00	1.00
	Specificity	0.97	0.38	0.38	0.74	0.71	0.74
	Kappa	0.98	0.32	0.32	0.71	0.68	0.71
	TSS	0.97	0.38	0.38	0.74	0.71	0.74
10%TP	Sensitivity	0.77	1.00	0.90	1.00	1.00	1.00
	Specificity	0.98	0.50	0.56	0.85	0.85	0.85
	Kappa	0.90	0.46	0.49	0.85	0.85	0.85
	TSS	0.75	0.50	0.46	0.85	0.85	0.85
MaxSS	Sensitivity	0.87	1.00	1.00	1.00	1.00	1.00
	Specificity	0.97	0.50	0.44	0.85	0.85	0.85
	Kappa	0.92	0.46	0.39	0.85	0.85	0.85
	TSS	0.83	0.50	0.44	0.85	0.85	0.85
		Hoplobatrachus occipitalis					
MTP	Sensitivity	0.99	1.00	1.00	1.00	0.96	1.00
	Specificity	0.89	0.29	0.31	0.58	0.60	0.71
	Kappa	0.91	0.23	0.25	0.60	0.61	0.75
	TSS	0.88	0.29	0.31	0.58	0.56	0.71
10%TP	Sensitivity	0.84	0.93	0.93	0.89	0.85	0.96
	Specificity	1.00	0.71	0.67	0.89	0.91	0.78
	Kappa	0.91	0.69	0.64	0.86	0.86	0.79
	TSS	0.84	0.64	0.60	0.78	0.76	0.74
MaxSS	Sensitivity	0.94	1.00	1.00	0.89	0.85	0.96
	Specificity	0.98	0.44	0.44	0.89	0.91	0.80
	Kappa	0.95	0.40	0.40	0.86	0.86	0.81
	TSS	0.92	0.44	0.44	0.78	0.76	0.76
		Procavia capensis					
MTP	Sensitivity	0.95	0.80	0.80	1.00	1.00	1.00
	Specificity	0.60	0.50	0.55	1.00	0.95	0.95
	Kappa	0.59	0.36	0.42	1.00	0.96	0.96
	TSS	0.55	0.30	0.35	1.00	0.95	0.95
10%TP	Sensitivity	0.89	0.80	0.80	1.00	1.00	1.00
	Specificity	0.76	0.68	0.64	1.00	0.95	1.00
	Kappa	0.74	0.60	0.54	1.00	0.96	1.00
	TSS	0.66	0.48	0.44	1.00	0.95	1.00
MaxSS	Sensitivity	0.78	0.80	0.80	1.00	1.00	1.00
	Specificity	0.87	0.77	0.82	0.95	0.91	0.95
	Kappa	0.79	0.72	0.77	0.96	0.92	0.96
	TSS	0.65	0.57	0.62	0.95	0.91	0.95

Appendix B - Ecological niche models performance to ecologically plastic species

Appendix B.1: Bibliographic references from where observations were collected

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Table B.1 - Number of non-spatially aggregated observations (N) of *Papio papio* used for training (Train) and validations (Val) datasets and for each training area: West Africa (WA), and the Sahelian acacia savannah (SAS), West sudanian savannah (WSS), and Afrotropical (AFR). The value of the Nearest Neighbor Index (NNI) and the associate p-value (p) for each dataset.

	WA		SAS		WSS		AFR	
	Train	Val	Train	Val	Train	Val	Train	Val
N	50	29	27	8	23	18	27	19
NNI	0.86	0.80	0.81	1.18	1.12	0.75	0.80	0.84
p	0.60	0.05	0.07	0.30	0.26	0.05	0.07	0.19

Table B.2- Number of observations of the *Papio papio* used to train (N Train), test (N Test), and validate (N Valid) four maximum entropy model types, and average and standard deviation of training and test AUC of each model. The models were West Africa (WA), and the Sahelian acacia savannah (SAS), West sudanian savannah (WSS), and Afrotropical (AFR).

	N train	N test	N Valid	AUC (SD)	Test AUC (SD)
SAS	25	2	8	1.00 (0.00)	0.99 (0.01)
WSS	21	2	18	0.92 (0.04)	0.88 (0.15)
AFR	25	2	19	0.95 (0.06)	0.81 (0.24)
WA	45	4	29	0.93 (0.07)	0.84 (0.13)

Table B.3 - : Measures of contribution of environmental variables to the ecological models of *Papio papio*. Percentage of contribution (% Cont) and permutation importance (Perm) derived from maximum entropy models are given. Models derived were the West Africa (WA), and the Sahelian acacia savannah (SAS), West sudanian savannah (WSS), and Afrotropical (AFR). Explanation of variable codes is given in Table 3.4.

	SAS		WSS		AFR		WA	
	% Cont	Perm	% Cont	Perm	% Cont	Perm	% Cont	Perm
ATEM	0.08	0.00	6.18	1.77	0.73	0.60	0.94	2.41
MTEM	0.81	0.27	11.36	2.21	4.66	6.09	0.89	0.92
PWET	1.10	0.30	3.83	4.69	2.90	1.93	2.99	7.42
PET	0.39	0.26	1.65	1.24	4.95	4.03	5.16	5.99
SLOP	5.58	0.70	2.92	2.86	5.19	6.68	5.86	4.53
CROP	0.69	2.81	13.39	7.34	6.25	7.92	2.58	12.63
VECR	3.20	10.25	3.25	4.53	3.50	5.66	2.17	3.61
COSH	1.22	3.38	1.94	3.70	8.16	2.73	5.06	16.78
COHE	2.71	11.86	13.66	18.77	12.31	13.15	5.64	9.37
FBWV	0.03	0.20	10.21	7.24	9.26	3.76	6.88	3.82
BARE	0.66	0.24	4.74	5.38	8.05	4.54	1.72	3.48
WABO	0.34	1.19	4.66	1.43	18.99	2.74	3.16	1.30
PERM	66.31	55.70	19.67	33.74	0.51	2.65	30.43	17.89
SEAS	16.87	12.85	2.55	5.10	14.55	37.52	26.52	9.87

Table B.4 - Niche overlap analysis according to Schoener's D (Schoener 1968) and I statistic (see Warren *et al*. 2008 for additional details). Comparisons where made between predicted models were: the Sahelian acacia savannah (SAS), West sudanian savannah (WSS), and Afrotropical (AFR) models. The niche overlap was also measure between West Africa (WA) and the combined model (Comb).

		I				
		SAL	WSS	AFR	WA	Comb
D	SAS	-	0.69	0.5	-	-
	WSS	0.48	-	0.93	-	-
	AFR	0.34	0.84	-	-	-
	WA	-	-	-	-	0.67
	Comb	-	-	-	0.53	-

Table B.5 - Area and percentage of suitable pixels for *Papio papio* predicted by combined model in total and within each country. Area and percentage of suitable pixels that overlap with each class of human population, in total and by country. Area and percentage of suitable area currently protected, in total and in each country.

	Combined model		Human population (people/km2)						Protected Areas	
			>50		5 - 50		< 5			
	Area (km2)	%	Area (km2)	%	Area (km2)	%	Area (km2)	%	Area (km2)	%
Suitable area	221576.11	21.20	18493.44	8.35	161059.07	72.70	41994.29	18.96	29463.18	13.29
By country										
Mauritania	8694.71	3.92	0.00	0.00	4850.78	3.01	3843.93	9.15	0.00	0.00
Mali	76176.74	34.38	0.84	0.01	53790.00	33.40	22386.00	53.31	7888.90	26.78
Senegal	70118.00	31.65	8750.00	47.31	45641.38	28.33	15726.71	37.45	14605.11	49.57
The Gambia	8668.75	3.91	5372.63	29.05	3296.12	2.05	0.00	0.00	241.24	0.82
Guinea-Bissau	17768.00	8.02	1927.41	10.42	15840.63	9.84	0.00	0.00	1449.96	4.92
Guinea	35914.00	16.21	2164.46	11.70	33738.50	20.95	10.89	0.03	2578.26	8.75
Ivory Coast	0.84	0.00	0.00	0.00	0.84	0.00	0.00	0.00	0.00	0.00
Liberia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sierra Leone	4170.61	1.88	257.16	1.40	3913.46	2.42	0.00	0.00	340.08	1.15

Appendix C - Local hotspots of biodiversity

Appendix C.1. - Photographs of gueltas

G01 Agmeimîne
Guelta (not observable) was dry at time of visit. *Amietophrynus xeros* were observed inside a well beside the *guelta.*
Photo: F Martínez-Freiría

G02 Ain El Berbera
Guelta (not observable) is surrounded by palm trees
Photo: JC Brito

G03 Amzouzef
Photo: JC Brito

G04 Aouînet Nanâga
Extremely small *guelta*
Photo: JC Brito

G06 Aouînet Tenbouckit
Python sebae in the foreground
Photo: JC Brito

G07 Ayoûn en Na'aj
Photo: JC Brito

G08 Bâfa
Photo: F Martínez-Freiría

G09 Bajai
Photo: JC Brito

G10 Ch'Bayer
Photo: JC Brito

G11 Daal
Guelta (not observable) located in the narrow valley
Photo: JC Brito

G12 Dâber
Photo: JC Brito

G13 Dâyet et Teila
Photo: F Martínez-Freiría

G15 El Barda
Photo: JC Brito

G16 El Ghâira
Photo: JC Brito

G17 El Gleitât
Sampling inside the nearly dry *guelta*
Photo: F Martínez-Freiría

G18 El Hnouk
Photo: F Martínez-Freiría

G19 El Housseînîya
Photo: F Martínez-Freiría

G20 El Khedia
Photo: JC Brito

G21 El Mefga
Photo: JC Brito

G22 Emreimida
Photo: N Sillero

G23 E-n-Guinâr
Photo: JC Brito

G25 Foum el Kour
Photo: F Martínez-Freiría

G26 Foum Goussas
Photo: F Martínez-Freiría

G27 Galoûla
Photo: Z Boratyński

G28 Gamra Ouarbî
Photo: JC Brito

G29 Gânçai
Extremely small *guelta* (not observable) surrounded by dense vegetation
Photo: F Martínez-Freiría

G30 Garaouel
Photo: JC Brito

G31 Glât el Bil
Photo: JC Brito

G32 Gleitat Ej Jmel
Guelta was nearly dry at time of visit
Photo: JC Brito

G33 Goumbel
Photo: F Martínez-Freiría

G34 Gueltet Thor
Photo: JC Brito

G35 Guenétir
Photo: JC Brito

G36 Guérou
Guelta (not observable) is located in the bottom of the valley
Photo: JC Brito

G37 Guidemballa
Photo: F Martínez-Freiría

G38 Hamdoûn
Photo: JC Brito

G39 Jabara
Photo: F Martínez-Freiría

G40 Kabda
Photo: JC Brito.

G42 El Grâne
Guelta (not observable) is located inside the canyon in front
Photo: Z Boratyński.

G43 Laout
Photo: JC Brito

G44 Laout, 1km S of
Photo: JC Brito

G45 Legleyta
Guelta was nearly dry at time of visit
Photo: JC Brito

G46 Lemmollah
Photo: JC Brito

G47 Leouel
Photo: JC Brito

G48 Matmâta
Photo: Z Boratyński

G49 M'cherba
Photo: JC Brito

G50 Mendjoura
Photo: JC Brito

G51 Metraoucha
Photo: F Martínez-Freiría

G52 Meyla
Photo: JC Brito

G53 Oumm el Arjam
Guelta (not observable) is located at right, close to the dense palm trees
Photo: F Martínez-Freiría

G54 Oumm el Mhâr
Photo: JC Brito

G55 Oumm Icheglâne
Photo: JC Brito

G56 Oumm Icheglâne, 5km NW of
Guelta (not observable) is located in bottom of the valley
Photo: JC Brito

G57 Oumm Lemhâr
Photo: JC Brito

G58 Rh' Zembou
Photo: JC Brito

G59 Soufa
Photo: JC Brito

G61 Taorta
Photo: JC Brito

G62 Tartêga
Photo: JC Brito

G63 Tartêga, upstream of
Photo: JC Brito

G64 Taoujafet
Photo: JC Brito

G65 Terjît
Photo: JC Brito

G66 Tin Waadine
Guelta was dry at time of visit
Photo: JC Brito

G67 Tkhsutin
Photo: JC Brito

G68 Toumbahjît
Photo: JC Brito

G69 Toûngâd
Guelta (not observable) is surrounded by dense vegetation
Photo: F Martínez-Freiría

Table C.1 - Gueltas name, code and mountain. Seasonality character of each guelta.

Code	Name	Mountain	Seasonality
G01	Agmeimîne	Adrar Atar	Seasonal
G02	Ain El Berbera	Afollé	Seasonal
G03	Amzouzef	Tagant	Permanent
G04	Aouînet Nanâga	Assaba	Seasonal
G05	Aouînet Teidoûma	Tagant	Seasonal
G06	Aouînet Tenbouckit	Assaba	Seasonal
G07	Ayoûn en Na'aj	Afollé	Permanent
G08	Bâfa	Assaba	Seasonal
G09	Bajai	Tagant	Permanent
G10	Ch'Bayer	Tagant	Permanent
G11	Daal	Tagant	Seasonal
G12	Dâber	Tagant	Permanent
G13	Dâyet et Teila	Adrar Atar	Permanent
G14	Dekheïlet el ‘Aleïb (=Dekla, Ain Bâjed)	Tagant	Seasonal
G15	El Barda	Assaba	Permanent
G16	El Ghâira, source	Assaba	Permanent
G17	El Gleitât	Adrar Atar	Seasonal
G18	El Hnouk gorge	Adrar Atar	Seasonal
G19	El Housseînîya	Tagant	Permanent
G20	El Khedia	Tagant	Permanent
G21	El Mefga	Afollé	Permanent
G22	Emreimida	Tagant	Permanent
G23	E-n-Guinâr	Tagant	Seasonal
G24	Fanar	Tagant	Seasonal
G25	Foum el Kour	Tagant	Permanent
G26	Foum Goussas	Assaba	Permanent
G27	Galoûla	Assaba	Permanent
G28	Gamra Ouarbî	Tagant	Permanent
G29	Gânçai source	Assaba	Permanent
G30	Garaouel	Tagant	Permanent
G31	Glât el Bil	Adrar Atar	Seasonal
G32	Gleitat Ej Jmel	Tagant	Seasonal
G33	Goumbel	Assaba	Permanent
G34	Gueltet Thor	Assaba	Permanent
G35	Guenétir, source	Assaba	Permanent
G36	Guérou	Assaba	Seasonal
G37	Guidemballa	Assaba	Permanent
G38	Hamdoûn	Adrar Atar	Permanent
G39	Jabara	Tagant	Permanent
G40	Kabda	Tagant	Permanent

Code	Name	Mountain	Seasonality
G41	Kaimel	Tagant	Seasonal
G42	Kediet El Grâne	Assaba	Seasonal
G43	Laout	Tagant	Permanent
G44	Laout, 1km S of	Tagant	Permanent
G45	Legleyta	Assaba	Seasonal
G46	Lemmollah	Tagant	Seasonal
G47	Leouel	Tagant	Seasonal
G48	Matmâta	Tagant	Permanent
G49	M'cherba	Tagant	Permanent
G50	Mendjoura	Tagant	Seasonal
G51	Metraoucha	Afollé	Permanent
G52	Meyla	Assaba	Permanent
G53	Oumm el Arjam	Tagant	Seasonal
G54	Oumm el Mhâr	Afollé	Permanent
G55	Oumm Icheglâne	Assaba	Permanent
G56	Oumm Icheglâne, 5km NW of	Assaba	Seasonal
G57	Oumm Lemhâr (=Molomhar)	Adrar Atar	Permanent
G58	Rh' Zembou	Tagant	Permanent
G59	Soufa, oued	Assaba	Permanent
G60	Suklan	Tagant	Seasonal
G61	Taorta	Tagant	Seasonal
G62	Tartêga	Tagant	Permanent
G63	Tartêga, upstream of	Tagant	Permanent
G64	Taoujafet	Tagant	Seasonal
G65	Terjît, oasis	Adrar Atar	Permanent
G66	Tin Waadine	Tagant	Seasonal
G67	Tkhsutin	Tagant	Permanent
G68	Toumbahjît	Adrar Atar	Permanent
G69	Toûngâd	Adrar Atar	Permanent

Table C.2- Taxa present in gueltas. Taxa scientific and common name, biogeographic affinity and IUCN status

Group	Taxa	Common name	Affinity	IUCN	G01	G02	G03	G04	G05	G06	G07	G08	G09	G10	G11	G12
Amphibians	*Amietophrynus xeros*	Subdesert Toad	Sahelian endemic	LC	1	0	0	1	0	0	0	0	0	0	0	0
Amphibians	*Hoplobatrachus cf. occipitalis*	Crowned Frog	Mauritania endemic	NE	0	0	0	1	1	1	0	1	0	1	0	0
Amphibians	*Hoplobatrachus occipitalis*	African Groove-crowned Frog	Afro-tropical	LC	0	1	0	0	0	0	1	0	0	0	0	0
Amphibians	*Kassina senegalensis*	Senegal Land Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Amphibians	*Phrynobatrachus spp.*	Puddle frog	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Amphibians	*Ptychadena spp.*	Grass frog	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Amphibians	*Tomopterna cryptotis*	Common Sand Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Acanthodactylus dumerili*	Duméril's Fringe-fingered Lizard	Sahara endemic	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti*	Bouet's Agama	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti C*	Bouet's Agama	Mauritania endemic	LC	0	0	0	1	1	0	0	0	0	0	0	0
Reptiles	*Agama boueti W*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boulengeri E*	Boulenger's Agama	Mauritania endemic	LC	0	1	0	0	0	0	1	0	0	0	0	0
Reptiles	*Agama boulengeri W*	Boulenger's Agama	Mauritania endemic	LC	0	0	1	1	1	1	0	0	1	1	1	1
Reptiles	*Atractaspis micropholis*	Sahelian Burrowing Asp	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Cerastes cerastes*	Saharan horned viper	Saharo-sindian	NE	0	0	1	0	0	0	0	0	0	0	0	0
Reptiles	*Chamaeleo africanus*	The Basilisk Chameleon	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Crocodylus suchus*	West African crocodile	Afro-tropical	NE	0	1	1	1	1	0	0	1	1	1	0	0
Reptiles	*Echis leucogaster*	White-bellied Carpet Viper	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Bamanophis dorri*	Dorr's racer	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Naja nigricollis*	Black-necked spitting cobra	Afro-tropical	NE	0	0	0	1	0	0	0	0	0	0	0	0
Reptiles	*Psammophis elegans*	Elegant Sand Racer	Afro-tropical	NE	0	0	0	1	0	0	0	0	0	0	0	0
Reptiles	*Ptyodactylus cf. togoensis*	Fan-fingered gecko	Mauritania endemic	NE	0	0	0	1	0	0	0	0	0	0	0	0
Reptiles	*Python sebae*	African rock python	Afro-tropical	NE	0	0	0	0	0	1	0	0	0	0	0	0
Reptiles	*Stenodactylus petrii*	Dune gecko	Sahara endemic	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Tarentola hoggarensis*	African Wall Gecko	Afro-tropical	NE	0	0	0	1	0	0	1	0	1	0	0	0
Reptiles	*Tarentola parvicarinata*	Sierra Leone Wall Gecko	Sahelian endemic	NE	1	1	1	1	1	1	1	0	1	1	1	1
Reptiles	*Trachylepis quinquetaeniata*	African Five-lined Skink	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Tropiocolotes tripolitanus*	Northern Sand Gecko	Sahara endemic	LC	1	0	0	1	0	1	1	0	0	0	0	0
Reptiles	*Uromastyx dispar*	Sudan Mastigure	Sahara endemic	NE	0	0	1	0	0	0	0	0	0	1	0	1
Reptiles	*Varanus exanthematicus*	Savannah Monitor	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Varanus niloticus*	Nile monitor	Afro-tropical	NE	0	1	1	0	0	0	0	0	1	0	0	1

					G13	G14	G15	G16	G17	G18	G19	G20	G21	G22	G23	G24
Group	*Taxa*	Common name	Affinity	IUCN												
Amphibians	*Amietophrynus xeros*	Subdesert Toad	Sahelian endemic	LC	0	0	1	0	0	1	1	1	1	0	0	0
Amphibians	*Hoplobatrachus cf. occipitalis*	Crowned Frog	Mauritania endemic	NE	0	0	1	1	0	0	1	1	1	0	1	0
Amphibians	*Hoplobatrachus occipitalis*	African Groove-crowned Frog	Afro-tropical	LC	0	0	0	0	1	0	0	0	0	0	0	0
Amphibians	*Kassina senegalensis*	Senegal Land Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Amphibians	*Phrynobatrachus spp.*	Puddle frog	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Amphibians	*Ptychadena spp.*	Grass frog	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Amphibians	*Tomopterna cryptotis*	Common Sand Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Acanthodactylus dumerili*	Duméril's Fringe-fingered Lizard	Sahara endemic	NE	1	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti*	Bouet's Agama	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti C*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	1	0	1	0
Reptiles	*Agama boueti W*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boulengeri E*	Boulenger's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	1	0	0	0
Reptiles	*Agama boulengeri W*	Boulenger's Agama	Mauritania endemic	LC	1	1	1	1	1	0	1	1	0	1	1	1
Reptiles	*Atractaspis micropholis*	Sahelian Burrowing Asp	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Cerastes cerastes*	Saharan horned viper	Saharo-sindian	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Chamaeleo africanus*	The Basilisk Chameleon	Afro-tropical	NE	0	0	0	0	0	0	0	0	1	0	0	0
Reptiles	*Crocodylus suchus*	West African crocodile	Afro-tropical	NE	0	0	0	1	0	0	1	1	1	1	1	0
Reptiles	*Echis leucogaster*	White-bellied Carpet Viper	Sahelian endemic	LC	0	0	1	0	0	0	0	0	0	0	0	0
Reptiles	*Bamanophis dorri*	Dorr's racer	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Naja nigricollis*	Black-necked spitting cobra	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Psammophis elegans*	Elegant Sand Racer	Afro-tropical	NE	0	0	1	0	0	0	0	0	0	0	0	0
Reptiles	*Ptyodactylus cf. togoensis*	Fan-fingered gecko	Mauritania endemic	NE	0	0	1	1	0	0	0	0	0	0	0	0
Reptiles	*Python sebae*	African rock python	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Stenodactylus petrii*	Dune gecko	Sahara endemic	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Tarentola hoggarensis*	African Wall Gecko	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Tarentola parvicarinata*	Sierra Leone Wall Gecko	Sahelian endemic	NE	0	1	1	1	1	0	1	1	1	1	1	0
Reptiles	*Trachylepis quinquetaeniata*	African Five-lined Skink	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Tropiocolotes tripolitanus*	Northern Sand Gecko	Sahara endemic	LC	0	0	1	1	0	0	0	0	0	0	0	0
Reptiles	*Uromastyx dispar*	Sudan Mastigure	Sahara endemic	NE	1	0	0	0	0	0	0	1	0	0	0	1
Reptiles	*Varanus exanthematicus*	Savannah Monitor	Afro-tropical	LC	0	0	1	0	0	0	0	0	0	0	0	0
Reptiles	*Varanus niloticus*	Nile monitor	Afro-tropical	NE	0	0	1	0	0	0	1	0	1	0	0	1

Group	Taxa	Common name	Affinity	IUCN	G25	G26	G27	G28	G29	G30	G31	G32	G33	G34	G35	G36
Amphibians	*Amietophrynus xeros*	Subdesert Toad	Sahelian endemic	LC	0	0	1	0	0	0	0	0	1	1	0	0
Amphibians	*Hoplobatrachus cf. occipitalis*	Crowned Frog	Mauritania endemic	NE	0	1	1	1	1	1	0	0	1	0	1	1
Amphibians	*Hoplobatrachus occipitalis*	African Groove-crowned Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	1	0	0
Amphibians	*Kassina senegalensis*	Senegal Land Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Amphibians	*Phrynobatrachus spp.*	Puddle frog	Afro-tropical	NE	0	0	1	0	0	0	0	0	0	0	0	0
Amphibians	*Ptychadena spp.*	Grass frog	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	1	0
Amphibians	*Tomopterna cryptotis*	Common Sand Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Acanthodactylus dumerili*	Duméril's Fringe-fingered Lizard	Sahara endemic	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti*	Bouet's Agama	Sahelian endemic	LC	0	0	0	0	0	1	0	0	0	0	0	0
Reptiles	*Agama boueti C*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti W*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0	1	0	0
Reptiles	*Agama boulengeri E*	Boulenger's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boulengeri W*	Boulenger's Agama	Mauritania endemic	LC	1	1	1	0	1	1	1	1	1	1	1	1
Reptiles	*Atractaspis micropholis*	Sahelian Burrowing Asp	Sahelian endemic	LC	0	0	0	0	0	0	0	0	1	0	0	0
Reptiles	*Cerastes cerastes*	Saharan horned viper	Saharo-sindian	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Chamaeleo africanus*	The Basilisk Chameleon	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Crocodylus suchus*	West African crocodile	Afro-tropical	NE	0	1	1	0	0	1	0	1	1	1	1	0
Reptiles	*Echis leucogaster*	White-bellied Carpet Viper	Sahelian endemic	LC	0	0	0	0	0	1	0	0	0	0	0	0
Reptiles	*Bamanophis dorri*	Dorr's racer	Afro-tropical	NE	0	0	0	0	0	1	0	0	0	0	0	0
Reptiles	*Naja nigricollis*	Black-necked spitting cobra	Afro-tropical	NE	0	0	1	0	0	0	0	0	0	0	0	0
Reptiles	*Psammophis elegans*	Elegant Sand Racer	Afro-tropical	NE	0	0	0	0	0	0	0	0	1	0	0	0
Reptiles	*Ptyodactylus cf. togoensis*	Fan-fingered gecko	Mauritania endemic	NE	0	1	1	0	0	0	0	0	1	0	0	0
Reptiles	*Python sebae*	African rock python	Afro-tropical	NE	0	1	1	0	0	0	0	0	0	0	0	0
Reptiles	*Stenodactylus petrii*	Dune gecko	Sahara endemic	NE	0	0	0	0	0	0	0	1	0	0	0	0
Reptiles	*Tarentola hoggarensis*	African Wall Gecko	Afro-tropical	NE	0	0	0	0	0	0	0	1	0	0	0	0
Reptiles	*Tarentola parvicarinata*	Sierra Leone Wall Gecko	Sahelian endemic	NE	0	1	1	0	1	0	0	1	1	1	0	1
Reptiles	*Trachylepis quinquetaeniata*	African Five-lined Skink	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Tropiocolotes tripolitanus*	Northern Sand Gecko	Sahara endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Uromastyx dispar*	Sudan Mastigure	Sahara endemic	NE	1	0	0	0	0	0	0	1	0	0	0	0
Reptiles	*Varanus exanthematicus*	Savannah Monitor	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Varanus niloticus*	Nile monitor	Afro-tropical	NE	1	0	1	1	0	1	0	0	1	1	0	0

Group	Taxa	Common name	Affinity	IUCN	G37	G38	G39	G40	G41	G42	G43	G44	G45	G46	G47	G48
Amphibians	*Amietophrynus xeros*	Subdesert Toad	Sahelian endemic	LC	0	0	1	0	0	0	1	1	0	0	0	1
Amphibians	*Hoplobatrachus cf. occipitalis*	Crowned Frog	Mauritania endemic	NE	1	0	1	0	0	0	1	1	1	0	1	1
Amphibians	*Hoplobatrachus occipitalis*	African Groove-crowned Frog	Afro-tropical	LC	0	1	0	0	0	0	0	0	0	0	0	0
Amphibians	*Kassina senegalensis*	Senegal Land Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Amphibians	*Phrynobatrachus spp.*	Puddle frog	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Amphibians	*Ptychadena spp.*	Grass frog	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Amphibians	*Tomopterna cryptotis*	Common Sand Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Acanthodactylus dumerili*	Duméril's Fringe-fingered Lizard	Sahara endemic	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti*	Bouet's Agama	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti C*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti W*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boulengeri E*	Boulenger's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boulengeri W*	Boulenger's Agama	Mauritania endemic	LC	1	0	1	1	1	1	1	1	0	1	1	1
Reptiles	*Atractaspis micropholis*	Sahelian Burrowing Asp	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Cerastes cerastes*	Saharan horned viper	Saharo-sindian	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Chamaeleo africanus*	The Basilisk Chameleon	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Crocodylus suchus*	West African crocodile	Afro-tropical	NE	1	0	1	1	0	0	0	0	1	0	0	1
Reptiles	*Echis leucogaster*	White-bellied Carpet Viper	Sahelian endemic	LC	0	0	0	0	0	0	1	1	0	0	0	0
Reptiles	*Bamanophis dorri*	Dorr's racer	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Naja nigricollis*	Black-necked spitting cobra	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Psammophis elegans*	Elegant Sand Racer	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Ptyodactylus cf. togoensis*	Fan-fingered gecko	Mauritania endemic	NE	0	0	1	0	0	0	1	1	0	0	0	1
Reptiles	*Python sebae*	African rock python	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Stenodactylus petrii*	Dune gecko	Sahara endemic	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Tarentola hoggarensis*	African Wall Gecko	Afro-tropical	NE	0	0	0	0	1	0	0	0	0	0	0	0
Reptiles	*Tarentola parvicarinata*	Sierra Leone Wall Gecko	Sahelian endemic	NE	1	0	1	1	1	1	1	1	1	1	0	1
Reptiles	*Trachylepis quinquetaeniata*	African Five-lined Skink	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Tropiocolotes tripolitanus*	Northern Sand Gecko	Sahara endemic	LC	1	0	0	0	0	0	0	0	0	1	0	0
Reptiles	*Uromastyx dispar*	Sudan Mastigure	Sahara endemic	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Varanus exanthematicus*	Savannah Monitor	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Varanus niloticus*	Nile monitor	Afro-tropical	NE	0	0	1	0	0	0	1	1	1	1	0	1

Group	Taxa	Common name	Affinity	IUCN	G49	G50	G51	G52	G53	G54	G55	G56	G57	G58	G59	G60
Amphibians	*Amietophrynus xeros*	Subdesert Toad	Sahelian endemic	LC	0	0	1	1	1	1	1	0	1	0	1	0
Amphibians	*Hoplobatrachus cf. occipitalis*	Crowned Frog	Mauritania endemic	NE	0	1	1	1	0	1	1	1	0	0	1	0
Amphibians	*Hoplobatrachus occipitalis*	African Groove-crowned Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	1	0	0	0
Amphibians	*Kassina senegalensis*	Senegal Land Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	1	0
Amphibians	*Phrynobatrachus spp.*	Puddle frog	Afro-tropical	NE	0	0	0	1	0	0	0	0	0	0	0	0
Amphibians	*Ptychadena spp.*	Grass frog	Afro-tropical	NE	0	0	0	1	0	0	0	0	0	0	0	0
Amphibians	*Tomopterna cryptotis*	Common Sand Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Acanthodactylus dumerili*	Duméril's Fringe-fingered Lizard	Sahara endemic	NE	0	1	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti*	Bouet's Agama	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti C*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti W*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boulengeri E*	Boulenger's Agama	Mauritania endemic	LC	0	0	1	0	0	1	0	0	0	0	0	0
Reptiles	*Agama boulengeri W*	Boulenger's Agama	Mauritania endemic	LC	1	1	0	1	1	0	1	1	1	1	1	1
Reptiles	*Atractaspis micropholis*	Sahelian Burrowing Asp	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	1	0
Reptiles	*Cerastes cerastes*	Saharan horned viper	Saharo-sindian	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Chamaeleo africanus*	The Basilisk Chameleon	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Crocodylus suchus*	West African crocodile	Afro-tropical	NE	1	0	1	1	0	1	1	1	0	1	1	1
Reptiles	*Echis leucogaster*	White-bellied Carpet Viper	Sahelian endemic	LC	0	0	0	1	0	0	0	0	0	0	0	0
Reptiles	*Bamanophis dorri*	Dorr's racer	Afro-tropical	NE	0	0	0	1	0	1	0	0	0	0	0	0
Reptiles	*Naja nigricollis*	Black-necked spitting cobra	Afro-tropical	NE	0	0	0	1	0	0	0	0	0	0	0	0
Reptiles	*Psammophis elegans*	Elegant Sand Racer	Afro-tropical	NE	0	0	0	0	0	0	1	1	0	0	1	0
Reptiles	*Ptyodactylus cf. togoensis*	Fan-fingered gecko	Mauritania endemic	NE	0	0	0	1	0	0	1	1	0	0	1	0
Reptiles	*Python sebae*	African rock python	Afro-tropical	NE	0	0	1	1	0	1	1	1	0	0	0	0
Reptiles	*Stenodactylus petrii*	Dune gecko	Sahara endemic	NE	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Tarentola hoggarensis*	African Wall Gecko	Afro-tropical	NE	1	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Tarentola parvicarinata*	Sierra Leone Wall Gecko	Sahelian endemic	NE	1	1	1	1	1	1	1	1	0	1	1	1
Reptiles	*Trachylepis quinquetaeniata*	African Five-lined Skink	Afro-tropical	NE	0	0	0	1	0	0	0	0	0	0	0	0
Reptiles	*Tropiocolotes tripolitanus*	Northern Sand Gecko	Sahara endemic	LC	0	0	0	0	0	0	0	0	0	0	1	0
Reptiles	*Uromastyx dispar*	Sudan Mastigure	Sahara endemic	NE	0	0	0	0	1	0	0	0	0	1	0	1
Reptiles	*Varanus exanthematicus*	Savannah Monitor	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Reptiles	*Varanus niloticus*	Nile monitor	Afro-tropical	NE	1	1	1	1	0	1	0	0	0	0	1	1

Group	Taxa	Common name	Affinity	IUCN	G61	G62	G63	G64	G65	G66	G67	G68	G69
Amphibians	*Amietophrynus xeros*	Subdesert Toad	Sahelian endemic	LC	0	1	0	1	1	0	0	1	1
Amphibians	*Hoplobatrachus cf. occipitalis*	Crowned Frog	Mauritania endemic	NE	0	1	1	0	0	1	1	0	0
Amphibians	*Hoplobatrachus occipitalis*	African Groove-crowned Frog	Afro-tropical	LC	0	0	0	0	1	0	0	1	0
Amphibians	*Kassina senegalensis*	Senegal Land Frog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0
Amphibians	*Phrynobatrachus spp.*	Puddle frog	Afro-tropical	NE	0	0	0	0	0	0	0	0	0
Amphibians	*Ptychadena spp.*	Grass frog	Afro-tropical	NE	0	0	0	0	0	0	0	0	0
Amphibians	*Tomopterna cryptotis*	Common Sand Frog	Afro-tropical	LC	0	0	0	1	0	0	0	0	0
Reptiles	*Acanthodactylus dumerili*	Duméril's Fringe-fingered Lizard	Sahara endemic	NE	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti*	Bouet's Agama	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti C*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boueti W*	Bouet's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boulengeri E*	Boulenger's Agama	Mauritania endemic	LC	0	0	0	0	0	0	0	0	0
Reptiles	*Agama boulengeri W*	Boulenger's Agama	Mauritania endemic	LC	1	1	1	1	1	1	1	0	1
Reptiles	*Atractaspis micropholis*	Sahelian Burrowing Asp	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0
Reptiles	*Cerastes cerastes*	Saharan horned viper	Saharo-sindian	NE	0	0	0	0	0	0	0	0	0
Reptiles	*Chamaeleo africanus*	The Basilisk Chameleon	Afro-tropical	NE	0	0	0	0	0	0	0	0	0
Reptiles	*Crocodylus suchus*	West African crocodile	Afro-tropical	NE	1	1	1	0	0	1	1	0	0
Reptiles	*Echis leucogaster*	White-bellied Carpet Viper	Sahelian endemic	LC	1	0	0	0	0	1	0	0	0
Reptiles	*Bamanophis dorri*	Dorr's racer	Afro-tropical	NE	0	0	0	0	0	0	0	0	0
Reptiles	*Naja nigricollis*	Black-necked spitting cobra	Afro-tropical	NE	0	0	0	0	0	0	0	0	0
Reptiles	*Psammophis elegans*	Elegant Sand Racer	Afro-tropical	NE	0	0	0	0	0	0	0	0	0
Reptiles	*Ptyodactylus cf. togoensis*	Fan-fingered gecko	Mauritania endemic	NE	0	1	1	0	0	1	0	0	0
Reptiles	*Python sebae*	African rock python	Afro-tropical	NE	0	0	0	0	0	0	0	0	0
Reptiles	*Stenodactylus petrii*	Dune gecko	Sahara endemic	NE	0	0	0	0	0	0	0	0	0
Reptiles	*Tarentola hoggarensis*	African Wall Gecko	Afro-tropical	NE	1	1	1	0	0	1	0	0	0
Reptiles	*Tarentola parvicarinata*	Sierra Leone Wall Gecko	Sahelian endemic	NE	1	1	1	0	1	1	1	0	0
Reptiles	*Trachylepis quinquetaeniata*	African Five-lined Skink	Afro-tropical	NE	0	0	0	0	0	0	0	0	0
Reptiles	*Tropiocolotes tripolitanus*	Northern Sand Gecko	Sahara endemic	LC	1	0	0	0	0	0	0	0	0
Reptiles	*Uromastyx dispar*	Sudan Mastigure	Sahara endemic	NE	1	0	0	0	0	1	1	0	0
Reptiles	*Varanus exanthematicus*	Savannah Monitor	Afro-tropical	LC	0	0	0	0	0	1	0	0	0
Reptiles	*Varanus niloticus*	Nile monitor	Afro-tropical	NE	0	1	1	0	0	1	1	0	0

Group	*Taxa*	Common name	Affinity	IUCN	G01	G02	G03	G04	G05	G06	G07	G08	G09	G10	G11	G12
Fishes	*Barbus sp.*	Barb	NA	NE	0	0	0	1	1	0	0	0	0	0	0	0
Fishes	*Brycinus nurse*	Nurse Tetra	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Fishes	*Clarias anguillaris*	Eel Catfish	Afro-tropical	NE	0	0	0	0	0	0	0	1	0	0	0	0
Fishes	*Sarotherodon spp.*	Tilapia	NA	NE	0	0	0	0	0	0	0	1	0	0	0	0
Fishes	*Schilbe sp.*	African butter catfish	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Acomys airensis*	Western Saharan Spiny Mouse	Sahelian endemic	LC	0	0	0	0	0	0	1	0	0	0	0	0
Mammals	*Asellia tridens*	Geoffroy's Trident Leaf-nosed Bat	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Atelerix albiventris*	Four-toed Hedgehog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Canis aureus*	Golden Jackal	Saharo-sindian	LC	0	0	1	0	1	0	0	1	1	1	0	0
Mammals	*Civettictis civetta*	African Civet	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Erythrocebus patas*	Erythrocebus patas	Afro-tropical	LC	0	0	0	0	0	0	1	1	0	0	0	0
Mammals	*Felis caracal*	Caracal	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Felovia vae*	Felou Gundi	Mauritania endemic	DD	0	0	0	1	0	1	1	0	1	0	1	1
Mammals	*Genetta genetta*	Common Genet	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Herpestes sanguinea*	Slender Mongoose	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Hystrix cristata*	Crested Porcupine	Afro-tropical	LC	0	0	0	0	1	0	1	0	0	0	0	0
Mammals	*Ichneumia albicauda*	White-tailed Mongoose	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Lepus sp.*	African hare	Palaearctic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Mellivora capensis*	Honey Badger	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Papio papio*	Guinea baboon	Afro-tropical	NT	0	1	0	1	1	0	1	1	1	0	0	0
Mammals	*Paraechinus aethiopicus*	Desert Hedgehog	Saharo-sindian	LC	0	0	0	0	0	0	1	0	0	0	0	0
Mammals	*Phacochoerus africanus*	Common Warthog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Praomys sp.*	Long-footedd rat	Afro-tropical	LC	0	0	0	0	0	0	1	0	0	0	0	0
Mammals	*Procavia capensis*	Rock Hyrax	Afro-tropical	LC	0	1	0	1	0	0	1	0	1	0	1	1
Mammals	*Rhinopoma hardwickei*	Lesser Mouse-tailed Bat	Saharo-sindian	LC	0	0	0	0	0	0	0	0	1	0	0	0
Mammals	*Vulpes pallida*	Pale Fox	Sahelian endemic	DD	0	0	0	1	0	0	0	0	0	0	0	0
Mammals	*Vulpes rueppellii*	Rüppel's Fox	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Xerus erythropus*	Striped Ground Squirrel	Afro-tropical	LC	0	0	0	0	0	0	1	0	0	0	0	0

Group	*Taxa*	Common name	Affinity	IUCN	G13	G14	G15	G16	G17	G18	G19	G20	G21	G22	G23	G24
Fishes	*Barbus sp.*	Barb	NA	NE	1	0	0	0	1	0	0	0	0	0	1	0
Fishes	*Brycinus nurse*	Nurse Tetra	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Fishes	*Clarias anguillaris*	Eel Catfish	Afro-tropical	NE	0	0	0	0	0	0	1	0	0	0	0	0
Fishes	*Sarotherodon spp.*	Tilapia	NA	NE	0	0	0	0	0	0	0	0	0	0	0	0
Fishes	*Schilbe sp.*	African butter catfish	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Acomys airensis*	Western Saharan Spiny Mouse	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Asellia tridens*	Geoffroy's Trident Leaf-nosed Bat	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Atelerix albiventris*	Four-toed Hedgehog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Canis aureus*	Golden Jackal	Saharo-sindian	LC	0	0	1	0	0	0	0	0	1	0	1	0
Mammals	*Civettictis civetta*	African Civet	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Erythrocebus patas*	Erythrocebus patas	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Felis caracal*	Caracal	Afro-tropical	LC	0	0	1	0	0	0	0	0	0	0	0	0
Mammals	*Felovia vae*	Felou Gundi	Mauritania endemic	DD	0	1	1	0	0	0	1	0	1	0	0	0
Mammals	*Genetta genetta*	Common Genet	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Herpestes sanguinea*	Slender Mongoose	Afro-tropical	LC	0	0	1	0	0	0	0	0	0	0	0	0
Mammals	*Hystrix cristata*	Crested Porcupine	Afro-tropical	LC	0	1	0	0	0	0	1	0	1	0	1	0
Mammals	*Ichneumia albicauda*	White-tailed Mongoose	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Lepus sp.*	African hare	Palaearctic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Mellivora capensis*	Honey Badger	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Papio papio*	Guinea baboon	Afro-tropical	NT	0	0	1	0	0	0	0	0	0	0	1	1
Mammals	*Paraechinus aethiopicus*	Desert Hedgehog	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Phacochoerus africanus*	Common Warthog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Praomys sp.*	Long-footedd rat	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Procavia capensis*	Rock Hyrax	Afro-tropical	LC	0	0	0	0	0	0	1	1	1	0	0	0
Mammals	*Rhinopoma hardwickei*	Lesser Mouse-tailed Bat	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Vulpes pallida*	Pale Fox	Sahelian endemic	DD	0	0	0	0	0	0	0	0	0	0	0	1
Mammals	*Vulpes rueppellii*	Rüppel's Fox	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Xerus erythropus*	Striped Ground Squirrel	Afro-tropical	LC	0	1	0	0	0	0	1	0	0	0	0	1

Group	*Taxa*	Common name	Affinity	IUCN	G25	G26	G27	G28	G29	G30	G31	G32	G33	G34	G35	G36
Fishes	*Barbus sp.*	Barb	NA	NE	0	0	0	0	1	1	1	0	0	0	0	0
Fishes	*Brycinus nurse*	Nurse Tetra	Afro-tropical	NE	0	0	0	0	0	0	0	0	1	0	0	0
Fishes	*Clarias anguillaris*	Eel Catfish	Afro-tropical	NE	0	1	0	0	0	1	0	0	1	1	1	0
Fishes	*Sarotherodon spp.*	Tilapia	NA	NE	0	1	1	0	0	0	0	0	1	0	1	0
Fishes	*Schilbe sp.*	African butter catfish	Afro-tropical	NE	0	0	0	0	0	0	0	0	1	0	0	0
Mammals	*Acomys airensis*	Western Saharan Spiny Mouse	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Asellia tridens*	Geoffroy's Trident Leaf-nosed Bat	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	1	0
Mammals	*Atelerix albiventris*	Four-toed Hedgehog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Canis aureus*	Golden Jackal	Saharo-sindian	LC	0	0	1	0	0	1	0	1	1	0	0	0
Mammals	*Civettictis civetta*	African Civet	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Erythrocebus patas*	Erythrocebus patas	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	1	0
Mammals	*Felis caracal*	Caracal	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Felovia vae*	Felou Gundi	Mauritania endemic	DD	0	1	1	1	1	1	0	1	1	0	1	0
Mammals	*Genetta genetta*	Common Genet	Afro-tropical	LC	0	1	0	0	0	0	0	0	0	1	0	0
Mammals	*Herpestes sanguinea*	Slender Mongoose	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Hystrix cristata*	Crested Porcupine	Afro-tropical	LC	0	0	0	0	0	0	0	0	1	0	0	0
Mammals	*Ichneumia albicauda*	White-tailed Mongoose	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Lepus sp.*	African hare	Palaearctic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Mellivora capensis*	Honey Badger	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Papio papio*	Guinea baboon	Afro-tropical	NT	1	1	1	0	1	1	0	0	1	0	1	1
Mammals	*Paraechinus aethiopicus*	Desert Hedgehog	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Phacochoerus africanus*	Common Warthog	Afro-tropical	LC	0	0	0	0	0	1	0	0	0	0	0	0
Mammals	*Praomys sp.*	Long-footedd rat	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Procavia capensis*	Rock Hyrax	Afro-tropical	LC	0	1	0	1	0	1	0	1	1	0	0	1
Mammals	*Rhinopoma hardwickei*	Lesser Mouse-tailed Bat	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Vulpes pallida*	Pale Fox	Sahelian endemic	DD	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Vulpes rueppellii*	Rüppel's Fox	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	1	0	0
Mammals	*Xerus erythropus*	Striped Ground Squirrel	Afro-tropical	LC	0	0	0	0	0	0	0	1	1	1	1	0

Group	*Taxa*	Common name	Affinity	IUCN	G37	G38	G39	G40	G41	G42	G43	G44	G45	G46	G47	G48
Fishes	*Barbus sp.*	Barb	NA	NE	0	1	0	0	0	0	0	0	0	0	1	0
Fishes	*Brycinus nurse*	Nurse Tetra	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Fishes	*Clarias anguillaris*	Eel Catfish	Afro-tropical	NE	1	0	1	0	0	0	0	0	0	0	0	1
Fishes	*Sarotherodon spp.*	Tilapia	NA	NE	1	0	0	0	0	0	0	0	0	0	0	0
Fishes	*Schilbe sp.*	African butter catfish	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Acomys airensis*	Western Saharan Spiny Mouse	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Asellia tridens*	Geoffroy's Trident Leaf-nosed Bat	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Atelerix albiventris*	Four-toed Hedgehog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Canis aureus*	Golden Jackal	Saharo-sindian	LC	0	0	1	1	0	0	1	1	1	0	0	1
Mammals	*Civettictis civetta*	African Civet	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Erythrocebus patas*	Erythrocebus patas	Afro-tropical	LC	0	0	1	0	0	0	0	0	0	0	0	1
Mammals	*Felis caracal*	Caracal	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Felovia vae*	Felou Gundi	Mauritania endemic	DD	1	1	1	0	0	1	1	1	0	1	0	1
Mammals	*Genetta genetta*	Common Genet	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Herpestes sanguinea*	Slender Mongoose	Afro-tropical	LC	0	0	0	0	0	1	0	0	0	0	0	0
Mammals	*Hystrix cristata*	Crested Porcupine	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	1	0
Mammals	*Ichneumia albicauda*	White-tailed Mongoose	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Lepus sp.*	African hare	Palaearctic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Mellivora capensis*	Honey Badger	Afro-tropical	LC	0	0	0	0	0	0	0	0	1	0	0	0
Mammals	*Papio papio*	Guinea baboon	Afro-tropical	NT	0	0	1	0	0	1	1	1	1	0	0	1
Mammals	*Paraechinus aethiopicus*	Desert Hedgehog	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Phacochoerus africanus*	Common Warthog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Praomys sp.*	Long-footedd rat	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Procavia capensis*	Rock Hyrax	Afro-tropical	LC	0	1	1	0	0	0	1	1	0	0	1	1
Mammals	*Rhinopoma hardwickei*	Lesser Mouse-tailed Bat	Saharo-sindian	LC	0	0	1	0	0	0	0	0	0	0	0	1
Mammals	*Vulpes pallida*	Pale Fox	Sahelian endemic	DD	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Vulpes rueppellii*	Rüppel's Fox	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Xerus erythropus*	Striped Ground Squirrel	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0

					G49	G50	G51	G52	G53	G54	G55	G56	G57	G58	G59	G60
Group	*Taxa*	Common name	Affinity	IUCN												
Fishes	*Barbus sp.*	Barb	NA	NE	0	1	0	0	0	1	0	0	1	0	0	0
Fishes	*Brycinus nurse*	Nurse Tetra	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Fishes	*Clarias anguillaris*	Eel Catfish	Afro-tropical	NE	0	0	1	0	0	0	0	0	1	0	1	0
Fishes	*Sarotherodon spp.*	Tilapia	NA	NE	0	0	1	0	0	0	0	0	0	0	0	0
Fishes	*Schilbe sp.*	African butter catfish	Afro-tropical	NE	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Acomys airensis*	Western Saharan Spiny Mouse	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Asellia tridens*	Geoffroy's Trident Leaf-nosed Bat	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Atelerix albiventris*	Four-toed Hedgehog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Canis aureus*	Golden Jackal	Saharo-sindian	LC	1	0	1	0	0	0	0	0	1	1	1	0
Mammals	*Civettictis civetta*	African Civet	Afro-tropical	LC	0	0	0	0	0	1	0	0	0	0	0	0
Mammals	*Erythrocebus patas*	Erythrocebus patas	Afro-tropical	LC	0	0	0	1	0	0	0	0	0	0	0	0
Mammals	*Felis caracal*	Caracal	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Felovia vae*	Felou Gundi	Mauritania endemic	DD	1	0	0	1	0	1	0	1	1	0	1	1
Mammals	*Genetta genetta*	Common Genet	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Herpestes sanguinea*	Slender Mongoose	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Hystrix cristata*	Crested Porcupine	Afro-tropical	LC	0	0	0	1	0	0	0	0	0	0	1	1
Mammals	*Ichneumia albicauda*	White-tailed Mongoose	Afro-tropical	LC	0	0	0	0	0	1	0	0	0	0	0	0
Mammals	*Lepus sp.*	African hare	Palaearctic	LC	0	1	0	0	0	0	0	0	0	0	0	0
Mammals	*Mellivora capensis*	Honey Badger	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Papio papio*	Guinea baboon	Afro-tropical	NT	1	0	1	1	0	1	1	1	0	0	1	0
Mammals	*Paraechinus aethiopicus*	Desert Hedgehog	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Phacochoerus africanus*	Common Warthog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Praomys sp.*	Long-footedd rat	Afro-tropical	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Procavia capensis*	Rock Hyrax	Afro-tropical	LC	1	0	1	1	0	1	0	0	0	0	1	0
Mammals	*Rhinopoma hardwickei*	Lesser Mouse-tailed Bat	Saharo-sindian	LC	1	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Vulpes pallida*	Pale Fox	Sahelian endemic	DD	0	0	1	0	0	0	0	0	0	0	0	0
Mammals	*Vulpes rueppellii*	Rüppel's Fox	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0	0	0	0
Mammals	*Xerus erythropus*	Striped Ground Squirrel	Afro-tropical	LC	0	1	0	0	0	0	0	0	0	0	1	1

					G61	G62	G63	G64	G65	G66	G67	G68	G69
Group	*Taxa*	Common name	Affinity	IUCN									
Fishes	*Barbus sp.*	Barb	NA	NE	0	0	0	0	1	0	0	0	1
Fishes	*Brycinus nurse*	Nurse Tetra	Afro-tropical	NE	0	0	0	0	0	0	0	0	0
Fishes	*Clarias anguillaris*	Eel Catfish	Afro-tropical	NE	0	1	0	0	0	0	0	0	0
Fishes	*Sarotherodon spp.*	Tilapia	NA	NE	0	0	0	0	0	0	0	0	0
Fishes	*Schilbe sp.*	African butter catfish	Afro-tropical	NE	0	0	0	0	0	0	0	0	0
Mammals	*Acomys airensis*	Western Saharan Spiny Mouse	Sahelian endemic	LC	0	0	0	0	0	0	0	0	0
Mammals	*Asellia tridens*	Geoffroy's Trident Leaf-nosed Bat	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0
Mammals	*Atelerix albiventris*	Four-toed Hedgehog	Afro-tropical	LC	1	0	0	0	0	0	0	0	0
Mammals	*Canis aureus*	Golden Jackal	Saharo-sindian	LC	0	1	1	0	0	1	0	0	0
Mammals	*Civettictis civetta*	African Civet	Afro-tropical	LC	0	0	0	0	0	0	0	0	0
Mammals	*Erythrocebus patas*	Erythrocebus patas	Afro-tropical	LC	0	1	1	0	0	0	0	0	0
Mammals	*Felis caracal*	Caracal	Afro-tropical	LC	0	0	0	0	0	0	0	0	0
Mammals	*Felovia vae*	Felou Gundi	Mauritania endemic	DD	1	1	1	1	1	1	1	0	1
Mammals	*Genetta genetta*	Common Genet	Afro-tropical	LC	0	0	0	0	0	0	0	0	0
Mammals	*Herpestes sanguinea*	Slender Mongoose	Afro-tropical	LC	0	0	0	0	0	0	0	0	0
Mammals	*Hystrix cristata*	Crested Porcupine	Afro-tropical	LC	1	0	0	0	0	1	1	0	0
Mammals	*Ichneumia albicauda*	White-tailed Mongoose	Afro-tropical	LC	0	0	0	0	0	0	0	0	0
Mammals	*Lepus sp.*	African hare	Palaearctic	LC	0	0	0	0	0	0	0	0	0
Mammals	*Mellivora capensis*	Honey Badger	Afro-tropical	LC	0	0	0	0	0	0	0	0	0
Mammals	*Papio papio*	Guinea baboon	Afro-tropical	NT	0	1	1	0	0	0	0	0	0
Mammals	*Paraechinus aethiopicus*	Desert Hedgehog	Saharo-sindian	LC	0	0	0	1	0	0	0	0	0
Mammals	*Phacochoerus africanus*	Common Warthog	Afro-tropical	LC	0	0	0	0	0	0	0	0	0
Mammals	*Praomys sp.*	Long-footedd rat	Afro-tropical	LC	0	0	0	0	0	0	0	0	0
Mammals	*Procavia capensis*	Rock Hyrax	Afro-tropical	LC	0	1	1	0	1	0	0	0	0
Mammals	*Rhinopoma hardwickei*	Lesser Mouse-tailed Bat	Saharo-sindian	LC	0	1	1	0	0	0	0	0	0
Mammals	*Vulpes pallida*	Pale Fox	Sahelian endemic	DD	0	0	0	0	0	0	0	0	0
Mammals	*Vulpes rueppellii*	Rüppel's Fox	Saharo-sindian	LC	0	0	0	0	0	0	0	0	0
Mammals	*Xerus erythropus*	Striped Ground Squirrel	Afro-tropical	LC	0	0	0	0	0	0	1	0	0

Table C.3 - Number of species and endemics present in each guelta by taxonomic group and IUCN status. Sum of species present in gueltas of each mountain. Gueltas code and name. DD: Daevaluated; LC: Least concern; NT: Near threatened; VU: Vulnerable; CR: Critically Endangered.

Code	Guelta name	Fishes	Amphibians	Reptiles	Mammals	Total	Mauritania Endemics	DD	NE	LC	NT	VU	CR
G01	Agmeimîne	0	1	2	0	3	0	0	1	2	0	0	0
G13	Dâyet et Teila	1	0	3	0	4	1	0	3	1	0	0	0
G17	El Gleitât	1	1	2	0	4	1	0	2	2	0	0	0
G18	El Hnouk gorge	0	1	0	0	1	0	0	0	1	0	0	0
G31	Glât el Bil	1	0	1	0	2	1	0	1	1	0	0	0
G38	Hamdoûn	1	1	0	2	4	1	1	1	2	0	0	0
G57	Oumm Lemhâr (=Molomhar)	2	2	1	2	7	2	1	2	4	0	0	0
G65	Terjît, oasis	1	2	2	2	7	2	1	2	4	0	0	0
G68	Toumbahjît	0	2	0	0	2	0	0	0	2	0	0	0
G69	Toûngâd	1	1	1	1	4	2	1	1	2	0	0	0
Σ Adrar		2	2	5	3	12	2	1	5	6	0	0	0
G03	Amzouzef	0	0	6	1	7	1	0	5	2	0	0	0
G05	Aouînet Teidoûma	1	1	4	3	9	3	0	4	4	1	0	0
G09	Bajai	0	0	5	5	10	2	1	4	4	1	0	0
G10	Ch'Bayer	0	1	4	1	6	2	0	4	2	0	0	0
G11	Daal	0	0	2	2	4	2	1	1	2	0	0	0
G12	Dâber	0	0	4	2	6	2	1	3	2	0	0	0
G14	Dekheïlet el ‘Aleïb (=Dekla, Ain Bâjed)	0	0	2	3	5	2	1	1	3	0	0	0
G19	El Housseînîya	1	2	4	4	11	3	1	5	5	0	0	0
G20	El Khedia	0	2	4	1	7	2	0	4	3	0	0	0
G22	Emreimida	0	0	3	0	3	1	0	2	1	0	0	0
G23	E-n-Guinâr	1	1	4	3	9	3	0	4	4	1	0	0
G24	Fanar	0	0	3	3	6	1	1	2	2	1	0	0
G25	Foum el Kour	0	0	3	1	4	1	0	2	1	1	0	0
G28	Gamra Ouarbî	0	1	1	2	4	2	1	2	1	0	0	0
G30	Garaouel	2	1	6	5	14	3	1	6	6	1	0	0

Code	Guelta name	Fishes	Amphibians	Reptiles	Mammals	Total	Mauritania Endemics	DD	NE	LC	NT	VU	CR
G32	Gleitat Ej Jmel	0	0	6	4	10	2	1	5	4	0	0	0
G39	Jabara	1	2	5	6	14	4	1	6	6	1	0	0
G40	Kabda	0	0	3	1	4	1	0	2	2	0	0	0
G41	Kaimel	0	0	3	0	3	1	0	2	1	0	0	0
G43	Laout	0	2	5	4	11	4	1	4	5	1	0	0
G44	Laout, 1km S of	0	2	5	4	11	4	1	4	5	1	0	0
G46	Lemmollah	0	0	4	1	5	2	1	2	2	0	0	0
G47	Leouel	1	1	1	2	5	2	0	2	3	0	0	0
G48	Matmâta	1	2	5	6	14	4	1	6	6	1	0	0
G49	M'cherba	0	0	5	5	10	2	1	4	4	1	0	0
G50	Mendjoura	1	1	4	2	8	2	0	5	3	0	0	0
G53	Oumm el Arjam	0	1	3	0	4	1	0	2	2	0	0	0
G58	Rh' Zembou	0	0	4	1	5	1	0	3	2	0	0	0
G60	Suklan	0	0	5	3	8	2	1	4	3	0	0	0
G61	Taorta	0	0	7	3	10	2	1	4	5	0	0	0
G62	Tartêga	1	2	6	6	15	4	1	7	6	1	0	0
G63	Tartêga, upstream of	0	1	6	6	13	4	1	6	5	1	0	0
G64	Taoujafet	0	2	1	2	5	2	1	0	4	0	0	0
G66	Tin Waadine	0	1	9	3	13	4	1	7	5	0	0	0
G67	Tkhsutin	0	1	5	3	9	3	1	5	3	0	0	0
Σ Tagant		2	3	16	13	34	5	2	13	18	1	0	0
G04	Aouînet Nanâga	1	2	9	4	16	5	2	8	5	1	0	0
G06	Aouînet Tenbouckit	0	1	4	1	6	3	1	3	2	0	0	0
G08	Bâfa	2	1	1	3	7	1	0	4	2	1	0	0
G15	El Barda	0	2	8	5	15	4	1	5	8	1	0	0
G16	El Ghâira, source	0	1	5	0	6	3	0	4	2	0	0	0
G26	Foum Goussas	2	1	5	4	12	4	1	7	3	1	0	0
G27	Galoûla	1	3	7	3	14	4	1	9	3	1	0	0
G29	Gânçai source	1	1	2	2	6	3	1	3	1	1	0	0
G33	Goumbel	4	2	7	6	19	4	1	10	7	1	0	0
G34	Gueltet Thor	1	2	5	3	11	2	0	4	7	0	0	0
G35	Guenétir, source	2	2	2	5	11	3	1	5	4	1	0	0
G36	Guérou	0	1	2	2	5	2	0	2	2	1	0	0
G37	Guidemballa	2	1	4	1	8	3	1	5	2	0	0	0
G42	Kediet El Grâne	0	0	2	3	5	2	1	1	2	1	0	0

Code	Guelta name	Fishes	Amphibians	Reptiles	Mammals	Total	Mauritania Endemics	DD	NE	LC	NT	VU	CR
G45	Legleyta	0	1	3	3	7	1	0	4	2	1	0	0
G52	Meyla	0	4	10	5	19	4	1	11	6	1	0	0
G55	Oumm Icheglâne	0	2	6	1	9	3	0	6	2	1	0	0
G56	Oumm Icheglâne, 5km NW of	0	1	6	2	9	4	1	6	1	1	0	0
G59	Soufa, oued	1	3	8	6	18	4	1	7	9	1	0	0
Σ Assaba		5	6	17	14	42	6	2	18	21	1	0	0
G02	Ain El Berbera	0	1	4	2	7	1	0	3	3	1	0	0
G07	Ayoûn en Na'aj	0	1	4	9	14	2	1	2	10	1	0	0
G21	El Mefga	0	2	6	4	12	4	1	5	6	0	0	0
G51	Metraoucha	2	2	5	4	13	2	1	7	4	1	0	0
G54	Oumm el Mhâr	1	2	6	5	14	3	1	7	5	1	0	0
Σ Afollé		3	3	10	13	29	4	2	11	15	1	0	0

Appendix D - Sahara-Sahel functional groups vulnerability to future climate change

List D.1:

AmphibiaWeb (2014). AmphibiaWeb: Information on amphibian biology and conservation. Berkeley, California:. Available: http://amphibiaweb.org/. (Accessed: October 22 2014)

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Table D.1 - Spearman rank correlations between pairs of analyzed functional traits according to distance matrices. The analyzed functional traits were: Ther – Thermoregulation; Water - Water dependency; Hab - Habitat selection; Act – Activity; Repr – Reproduction; Diet – Diet; Ecor - Number of ecoregions; HomR - Home range size; BodyS - Body size; and Vol – Volant.

	Ther	**Water**	**Habi**	**Acti**	**Repr**	**Diet**	**Ecor**	**HomR**	**BodyS**	**Vol**
Ther	1									
Water	-0.003	1								
Habi	0.079*	-0.003	1							
Acti	0.090*	-0.008	0.063*	1						
Repr	0.677*	-0.028	-0.003 *	0.202*	1					
Diet	0.409*	-0.049	0.009	0.109*	0.432*	1				
Ecor	0.008*	-0.003	0.058*	-0.001	-0.006	0.027	1			
HomR	0.029*	-0.060	0.029	0.061*	0.052*	0.231	0.129*	1		
BodyS	0.208*	0.030	0.023	0.135*	0.152*	0.218*	0.034	0.193*	1	
Vol	0.073*	-0.039	0.048*	0.023*	-0.028	-0.019	-0.089	0.013	0.013	1

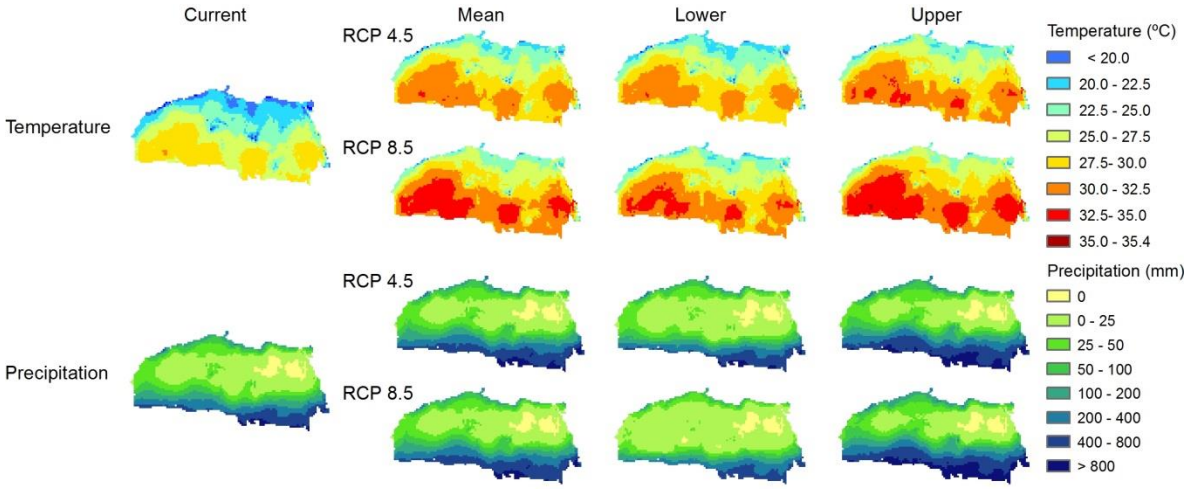

Fig. D.1 - Distribution patterns of annual mean temperature and precipitation in the Sahara-Sahel in the present and predicted for 2080 according to 10 GCMs and considering two RCP pathways. Upper and lower models represent the mean of the 10 GCMs added or subtracted by the standard deviation. Temperature and precipitation are annual mean temperature and precipitation, respectively.

Table D.2- : Groups' identification. Groups' name. Taxa within each group. Groups' description.

Group	Class	Taxa	Group description
EctNocS	Amphibia	*Amietophrynus kassasii*	Oviparous, ectothermics, mostly insectivorous, nocturnal, small home ranges
	Amphibia	*Kassina wazae*	
	Reptilia	*Atractaspis micropholis*	
	Reptilia	*Leptotyphlops algeriensis*	
	Reptilia	*Leptotyphlops boetti*	
	Reptilia	*Leptotyphlops cairi*	
	Reptilia	*Ptyodactylus siphonorhina*	
	Reptilia	*Tarentola boehmei*	
	Reptilia	*Tarentola chazaliae*	
	Reptilia	*Tarentola deserti*	
	Reptilia	*Tarentola mindiae*	
	Reptilia	*Tarentola neglecta*	
	Reptilia	*Telescopus hoogstraali*	
	Reptilia	*Tropiocolotes algericus*	
	Reptilia	*Tropiocolotes bisharicus*	
	Reptilia	*Tropiocolotes nattereri*	
	Reptilia	*Tropiocolotes nubicus*	
	Reptilia	*Tropiocolotes steudeneri*	
	Reptilia	*Tropiocolotes tripolitanus*	
	Reptilia	*Typhlops etheridgei*	
EndNocM	Mammalia	*Eptesicus floweri*	Viviparous, endothermics, nocturnal, medium home ranges
	Mammalia	*Ictonyx libyca*	
	Mammalia	*Pipistrellus deserti*	
	Mammalia	*Plecotus christii*	
	Mammalia	*Vulpes pallida*	
	Mammalia	*Vulpes zerda*	

Group	Class	Taxa	Group description
	Mammalia	*Acomys airensis*	
	Mammalia	*Acomys cahirinus*	
	Mammalia	*Acomys seurati*	
	Mammalia	*Crocidura lusitania*	
	Mammalia	*Crocidura pasha*	
	Mammalia	*Crocidura tarfayensis*	
	Mammalia	*Desmodilliscus braueri*	
	Mammalia	*Gerbillus amoenus*	
	Mammalia	*Gerbillus bottai*	
	Mammalia	*Gerbillus floweri*	
	Mammalia	*Gerbillus gerbillus*	
	Mammalia	*Gerbillus latastei*	
	Mammalia	*Gerbillus lowei*	
	Mammalia	*Gerbillus mackillingini*	Viviparous,
	Mammalia	*Gerbillus muriculus*	endothermics,
	Mammalia	*Gerbillus nancillus*	mostly
EndNocS	Mammalia	*Gerbillus nigeriae*	omnivorous,
	Mammalia	*Gerbillus perpallidus*	mostly nocturnal,
	Mammalia	*Gerbillus principulus*	small home
	Mammalia	*Gerbillus pyramidum*	ranges.
	Mammalia	*Gerbillus rosalinda*	
	Mammalia	*Gerbillus rupicola*	
	Mammalia	*Gerbillus stigmonyx*	
	Mammalia	*Gerbillus tarabuli*	
	Mammalia	*Gerbillus watersi*	
	Mammalia	*Grammomys aridulus*	
	Mammalia	*Lemniscomys hoogstraali*	
	Mammalia	*Mastomys kollmannspergeri*	
	Mammalia	*Sekeetamys calurus*	
	Mammalia	*Taterillus arenarius*	
	Mammalia	*Taterillus lacustris*	
	Mammalia	*Taterillus petteri*	
	Mammalia	*Taterillus tranieri*	

Group	Class	Taxa	Group description
	Reptilia	*Dasypeltis sahelensis*	
	Reptilia	*Echis leucogaster*	
	Reptilia	*Hemorrhois algirus*	
	Reptilia	*Naja nubiae*	
	Reptilia	*Psammophis aegyptius*	
	Reptilia	*Scincus albifasciatus*	
	Reptilia	*Stenodactylus petri*	
	Reptilia	*Stenodactylus stenodactylus*	Oviparous,
	Reptilia	*Trapelus boehmei*	ectothermics,
EctDiuM	Reptilia	*Trapelus mutabilis*	mostly diurnal,
	Reptilia	*Trapelus savignii*	medium home
	Reptilia	*Trapelus schmitzi*	ranges
	Reptilia	*Trapelus tournevillei*	
	Reptilia	*Uromastyx acanthinura*	
	Reptilia	*Uromastyx alfredschmidti*	
	Reptilia	*Uromastyx dispar*	
	Reptilia	*Uromastyx geyri*	
	Reptilia	*Uromastyx nigriventris*	
	Reptilia	*Uromastyx occidentalis*	
	Mammalia	*Addax nasomaculatus* -historical	
	Mammalia	*Ammotragus lervia*	
	Mammalia	*Ctenodactylus vali*	
	Mammalia	*Eudorcas rufifrons*	Viviparous,
	Mammalia	*Felovia vae*	endothermics,
EndDiuL	Mammalia	*Gazella cuvieri* - historical	herbivorous,
	Mammalia	*Gazella dorcas* - historical	diurnal, large
	Mammalia	*Gazella leptoceros* - historical	home ranges
	Mammalia	*Massoutiera mzabi*	
	Mammalia	*Nanger dama* - historical	
	Mammalia	*Psammomys vexillaris*	
	Aves	*Anthoscopus punctifrons*	
	Aves	*Caprimulgus eximius*	
	Aves	*Dendropicos elachus*	
	Aves	*Lamprotornis pulcher*	Oviparous,
	Aves	*Mirafra cordofanica*	endothermics,
EndDiuS	Aves	*Neotis nuba*	diurnal, small
	Aves	*Passer cordofanicus*	homes ranges,
	Aves	*Passer luteus*	volant
	Aves	*Prinia fluviatilis*	
	Aves	*Spiloptila clamans*	
	Aves	*Turdoides fulva*	

Group	Class	Taxa	Group description
	Reptilia	*Acanthodactylus aegyptius*	
	Reptilia	*Acanthodactylus aureus*	
	Reptilia	*Acanthodactylus dumerili*	
	Reptilia	*Acanthodactylus longipes*	
	Reptilia	*Acanthodactylus spinicauda*	
	Reptilia	*Acanthodactylus taghitensis*	
	Reptilia	*Agama boueti*	
	Reptilia	*Agama boulengeri*	
	Reptilia	*Agama tassiliensis*	
	Reptilia	*Chalcides boulengeri*	
	Reptilia	*Chalcides delislei*	Oviparous,
	Reptilia	*Chalcides humilis*	ectothermics,
EctDiuS	Reptilia	*Chalcides sepsoides*	insectivorous,
	Reptilia	*Chalcides sphenopsiformis*	diurnal, small
	Reptilia	*Hemidactylus foudaii*	home ranges.
	Reptilia	*Hemidactylus mindiae*	
	Reptilia	*Mesalina bahaeldini*	
	Reptilia	*Mesalina pasteuri*	
	Reptilia	*Mesalina rubropunctata*	
	Reptilia	*Philochortus lhotei*	
	Reptilia	*Philochortus zolii*	
	Reptilia	*Platyceps saharicus*	
	Reptilia	*Pristurus adrarensis*	
	Reptilia	*Scincopus fasciatus*	
	Reptilia	*Testudo kleinmanni*	

Table D.3 - Independent contributions of each analyzed functional trait to the global Gower's distance. Contribution is given by the correlation between squared distance matrices for each trait and the global squared distance. The analyzed functional traits were: Ther – Thermoregulation; Water - Water dependency; Hab - Habitat selection; Act – Activity; Repr – Reproduction; Diet – Diet; Ecor - Number of ecoregions; HomR - Home range size; BodyS - Body size; and Vol – Volant.

Traits	Global distance
Repr	0.69
Ther	0.68
Diet	0.63
Acti	0.43
HomR	0.37
BodyS	0.29
Habi	0.29
Vol	0.26
Ecor	0.25
Water	0.06

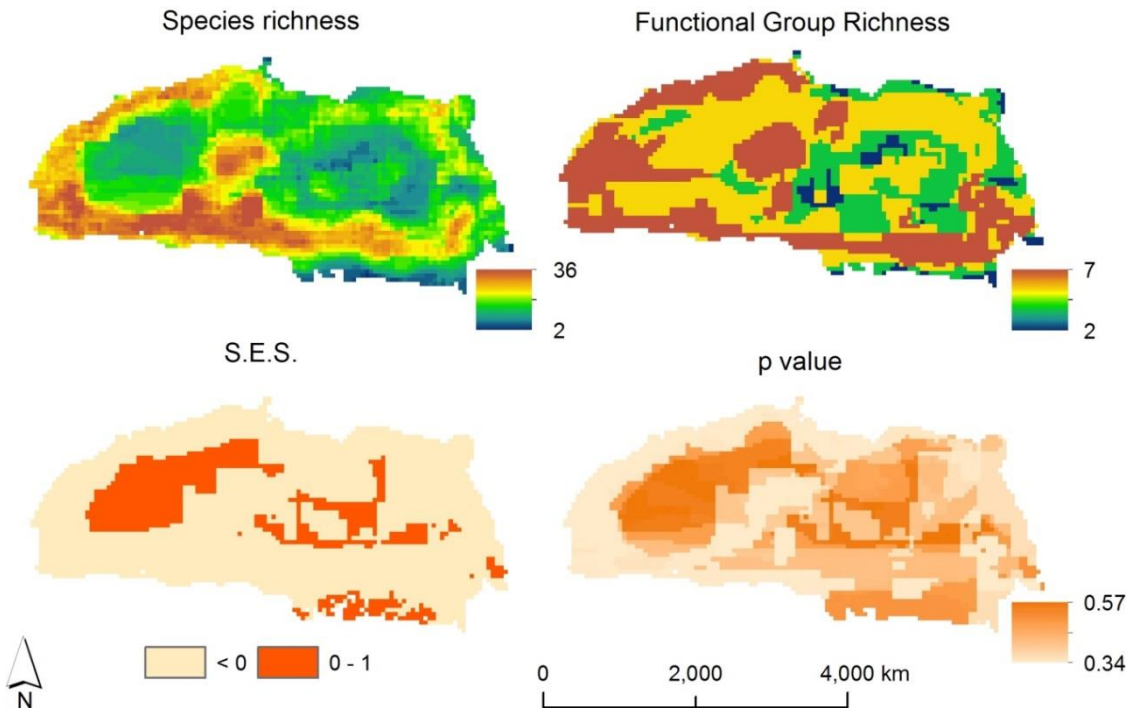

Fig. D. 2 - Distribution of endemic species richness, of observed functional group richness. Deviation from the null expectation (given an observed SR) for the functional group richness measured by the standardized effect sizes (SES). SES is given by (O − M)/S, where O is the observed value of functional group richness, and M and S are the expected mean and SD, respectively, after 999 randomizations for that pixel. Pixels with negative SESs exhibit richness lower than expected by chance, while with positive SESs exhibit higher richness. Significant deviations chance expectations are identified by p-value for each pixel.

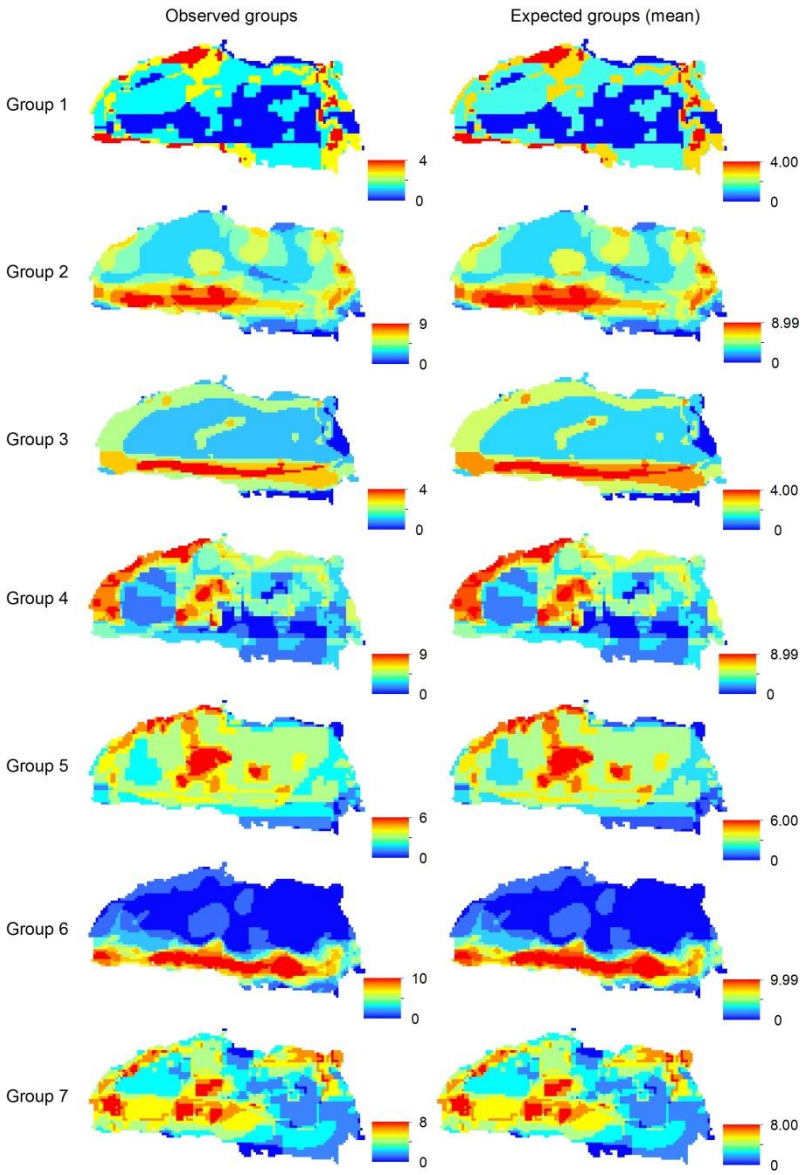

Fig. D.3 - Distribution of observed functional group richness and expected mean functional group richness if species were randomly selected from 999 randomizations for that pixel.

TableD.4 - Percentage of the current range of each functional group within protected areas, groups' area of occupancy not vulnerable, groups area of occupancy predicted to be vulnerable by magnitude of change in temperature, precipitation, and both factors together. %PA is the percentage of located inside current protected areas.

	Total in PA	Not vulnerable (PA)	Vulnerable (PA)		
			Temperature	Precipitation	Temp + Precip
EctNocS	6.4	32.3 (3.4)	4.2 (0.0)	67.0 (2.9)	3.5 (0.0)
EndNocS	5.9	1.3 (0.2)	34.7 (0.9)	93.0 (5.6)	28.9 (0.8)
EndNocM	6.0	24.1 (1.1)	38.1 (4.2)	49.5 (2.2)	11.7 (1.4)
EctDiuM	6.1	4.6 (0.1)	0.2 (0.2)	95.4 (6.0)	0.2 (0.2)
EndDiuL	8.9	7.2 (1.3)	7.9 (1.6)	89.7 (6.5)	4.8 (0.4)
EndDiuS	10.7	40.6 (2.7)	54.5 (7.9)	13.1 (2.1)	8.2 (1.9)
EctDiuS	5.1	0.0 (0.0)	13.5 (0.0)	100.0 (5.1)	13.5 (5.1)

Appendix E – Outreach activities and media coverage

Outreach activity at Serralves Museum. Talk and discussion about Vertebrates in Arid Environments - the case of Mauritania.

Interview to the National Radio Station (RDP) about mountain rock pools in deserts as local hotspots of biodiversity.

UNIVERSITY of WASHINGTON
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DESERTS TEEM WITH BIODIVERSITY, IF YOU KNOW WHERE TO LOOK

March 13, 2015 | *Conservation This Week* | *0 Comments*

California, or rather the California Floristic Province, is a global biodiversity hotspot. That means it hosts an incredibly large number of species of plants and animals found nowhere else on the planet. It is also threatened by environmental degradation. The same is true of the Tropical Andes, Brazil's Cerrado, the island of Madagascar, and the mountains of Central Asia, a range the early Persians referred to as the "roof of the world." Notably absent from most lists of biodiversity hotspots? Deserts.

At first, that is perhaps understandable. Deserts are typically thought of as lifeless wastelands, low in diversity both of plants and of animals. Life requires water, and deserts don't have much. But the truth is that deserts teem with life, if you know where to look, and, critically, when to look. The problem with most common approaches to identifying biodiversity hotspots is that they are defined at the global or continental levels. While deserts can be home to a tremendous amount of endemic species, they're usually clustered in very small localities, often around ephemeral sources of water.

Take the Sahara Desert, the largest warm desert on the planet. Together with the neighboring Sahel Desert, the Sahara-Sahel ecosystem hosts an impressive number of endemic species. The problem is they're restricted to a number of small and fragile humid habitats, tiny oases of life punctuating the vast expanse of desert. And human activities threaten those oases, seasonal rivers, and lakes. And that, in turn, threatens the species that have come to rely on them. "As such, those within the Sahara-Sahel may constitute local hotspots of biodiversity under threat," writes graduate student researcher Cândida Gomes Vale in a recent issue of *PLoS ONE*. Together with her colleagues, she's hoping to characterize

What's New
Conservation This Week

Invasive species might not be entirely awful, after all
May 8th, 2015

Citizen scientists track 'Ebola of the plant world'
May 7th, 2015

Dolphins are hunted for their teeth in the South Pacific
May 6th, 2015

the importance of mountain rock pools, called *gueltas*, in Mauritania.

Gueltas are tiny. They can be as small as just 100 square meters or so, and water is only present during the wet season, from July through September. Severe droughts in the 1970s have already rendered many of the northernmost gueltas in Mauritania completely dry year-round. As a result, many of the once-nomadic humans have become more sedentary around more predictable gueltas. That exacerbates the shortage of water in the dry season and results in fecal contamination by domestic animals. The wildlife that's come to rely on gueltas for survival is increasingly threatened.

Over several years, Vale assessed 69 different gueltas. Each guelta got a complete vertebrate biodiversity workup by no fewer than three researchers, along with nets, traps, and cameras. In addition to animals themselves, they took note of tracks, prints, burrows, and fecal deposits. Because animals don't usually sit still in one spot, the monitoring "zone" around each guelta extended two kilometers for fishes, amphibians, and reptiles, and five for mammals. The "surrounding area" extended fifty kilometers from the gueltas, thereby capturing information from mountain-dwelling animals who could potentially reach gueltas, corresponding to the likely maximum dispersal distance of any species occurring around the water. In addition, relying on a set of guidelines developed by the IUCN, Vale quantified both the type and number of threats affecting each individual guelta.

In all, Vale recorded 59 vertebrate species using gueltas, and there were no significant differences in animal presence from mountain to mountain. A whopping 78% of Mauritania's endemic species – those that are found there and nowhere else – were recorded visiting the gueltas. While they did not observe any species that the IUCN has classified as threatened, most of the species that use gueltas remain "Not Evaluated" by the IUCN, making the IUCN list fairly useless when it comes to identifying the conservation status of those animals. That's to say nothing of all the invertebrates, or the bats, which are also associated with the gueltas.

To put the numbers into perspective, four in five of the country's endemic species are contained in an area representing just 0.00004% of the country's surface area. "Gueltas are local hotspots of biodiversity deserving global attention," write the researchers. Only two-thirds of the gueltas the researchers visited had any sort of legal protection. Of those sites that the researchers deemed as conservation priorities, those numbers were worse: 80% are currently unprotected.

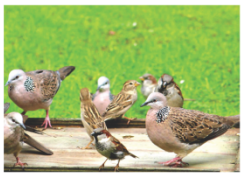
The problem is that Mauritania is also considered a "Low-Income Food-Deficit Country." Livestock play a crucial role for the people of the country, and they need land and water. So the solution is not to simply encircle all the gueltas in a national park. To simultaneously protect biodiversity and to enhance sustainable development, the researchers argue that the gueltas of highest conservation priority deserve protection, while channels could direct water to troughs further away, reducing both human and livestock pressure on them. "Such infrastructures would also allow decreasing [fecal] contamination of the water, contributing to public health," they say, as well as to wildlife health. And since the most easily accessible gueltas have crocodiles, the most charismatic of reptiles, there is a possibility for organized ecotourism as a means of infusing the area with added revenue.

The gueltas of the Sahara-Sahel are disproportionately important reservoirs of global biodiversity for their size and will likely become increasingly important refuges for wildlife in the face of climate change. Given that, perhaps they ought to be considered when making decisions about conservation priorities at the global or continental levels. **– Jason G. Goldman | 13 March 2015**

Source: Vale C.G., S.L. Pimm & J.C. Brito (2015). Overlooked Mountain Rock Pools in Deserts Are Critical Local Hotspots of Biodiversity, *PLOS ONE, 10* (2) e0118367. DOI: 10.1371/journal.pone.0118367.

Header image: Camels in a guelta in Chad, via Wikimedia Commons/Dario Menasce.

Tags: *biodiversity*, *deserts*, *livestock*, *water*



Beware of the backyard bird feeder
May 5th, 2015

Appendix F – Other publications

UNRAVELLING BIODIVERSITY, EVOLUTION AND THREATS TO CONSERVATION IN THE SAHARA-SAHEL[7]

[7] Brito, JC, Godinho, R, Martínez-Freiría, F, Pleguezuelos, JM, Rebelo, H, Santos, X, Vale, CG, Velo-Antón, G, Boratyński, Z, Carvalho, SB, Ferreira, S, Gonçalves, D V, Silva, TL, Tarroso, P, Campos, JC, Leite, JV, Nogueira, J, Álvares, F, Sillero, N, Sow, AS, Fahd, S, Crochet, P-A, Carranza, S (2014) Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel. Biological Reviews, 89, 215-31.

BIOLOGICAL REVIEWS
Cambridge Philosophical Society
Biol. Rev. (2014), **89**, pp. 215–231.
doi: 10.1111/brv.12049

Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel

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ABSTRACT

Deserts and arid regions are generally perceived as bare and rather homogeneous areas of low diversity. The Sahara is the largest warm desert in the world and together with the arid Sahel displays high topographical and climatic heterogeneity, and has experienced recent and strong climatic oscillations that have greatly shifted biodiversity distribution and community composition. The large size, remoteness and long-term political instability of the Sahara-Sahel, have limited knowledge on its biodiversity. However, over the last decade, there have been an increasing number of published scientific studies based on modern geomatic and molecular tools, and broad sampling of taxa of these regions. This review tracks trends in knowledge about biodiversity patterns, processes and threats across the Sahara-Sahel, and anticipates needs for biodiversity research and conservation. Recent studies are changing completely the perception of regional biodiversity patterns. Instead of relatively low species diversity with distribution covering most of the region, studies now suggest a high rate of endemism and larger number of species, with much narrower and fragmented ranges, frequently limited to micro-hotspots of biodiversity. Molecular-based studies are also unravelling cryptic diversity associated with mountains, which together with recent distribution atlases, allows identifying integrative biogeographic patterns in biodiversity distribution. Mapping of multivariate environmental variation (at 1 km × 1 km resolution) of the region illustrates main biogeographical features of the Sahara-Sahel and supports recently hypothesised dispersal corridors and refugia. Micro-scale water-features present mostly in mountains have been associated with local biodiversity hotspots. However, the distribution of available data on vertebrates highlights current knowledge gaps that still apply to a large proportion of the Sahara-Sahel. Current research is providing insights into key evolutionary and ecological processes, including causes and timing of radiation and divergence for multiple taxa, and associating the onset of the Sahara with diversification processes for low-mobility vertebrates. Examples of phylogeographic patterns are showing the importance of allopatric speciation in the Sahara-Sahel, and this review presents a synthetic overview of the most commonly hypothesised diversification mechanisms. Studies are also stressing that biodiversity is threatened by increasing human activities in the region, including overhunting and natural resources prospection, and in the future by predicted global warming. A representation of areas of conflict, landmines, and natural resources extraction illustrates how human activities and regional insecurity are hampering biodiversity research and

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conservation. Although there are still numerous knowledge gaps for the optimised conservation of biodiversity in the region, a set of research priorities is provided to identify the framework data needed to support regional conservation planning.

Key words: Africa, biodiversity, climate change, conservation, deserts, distribution, diversification, phylogeography, Sahara, Sahel.

CONTENTS

I. INTRODUCTION

Biodiversity is being eroded globally by habitat loss and climate change (Pimm, 2008). The challenges are to increase knowledge about species diversity and distribution (Whittaker *et al.*, 2005) and to detect the ecological and evolutionary processes behind them (Crandall *et al.*, 2000) in order to systematise biodiversity conservation planning (Margules & Pressey, 2000). Deserts [aridity index (average annual precipitation/potential evapo-transpiration) < 0.05; Ward, 2009] and arid regions (aridity index between 0.05 and 0.20) are generally perceived as bare and rather homogeneous areas of low diversity in comparison to other regions, thus attracting less scientific attention (Durant *et al.*, 2012). However, they allow examining the effects of extreme environments on biodiversity patterns (Ward, 2009). Deserts and arid regions present patchily distributed species whose range limits are under strong climatic control, a relatively high rate of endemism due to adaptive processes of organisms to extreme environments, locally endangered micro-hotspots of biodiversity (Dumont, 1982; Davies *et al.*, 2012; Murphy *et al.*, 2012; Wilson & Pitts, 2012), and climatic extremes generating sharp ecological gradients (Schulz *et al.*, 2009). Increasing human exploitation activities and progressive aridity conditions are negatively affecting desert biodiversity and also increasing poverty and the frequency of conflicts (McNeely, 2003; UNEP, 2006; Thorton *et al.*, 2008; Trape, 2009). The magnitude and velocity of climate change in deserts are predicted to be strong and fast (Loarie *et al.*, 2009), causing growing international awareness for desert biodiversity (McNeely, 2003; UNEP, 2006; Newby, 2007; Ward, 2009; Davies *et al.*, 2012; Durant *et al.*, 2012).

The Sahara desert and the neighbouring arid Sahel constitute two major ecoregions of the African continent (Olson *et al.*, 2001) and exhibit features that distinguish them from other world deserts and arid regions (Fig. 1):

(1) The Sahara is the largest warm desert in the world with land coverage, including the Sahel, of about 11230000 km^2 (larger than the Australian continent).

(2) There is high diversity of topographic features, from salt pans below sea level to high-altitude peaks (from −155 m at Lake Assal, Djibouti, to 3415 m at Emi Koussi, Chad) distributed along a system of 'mountain-sky islands' (UNEP, 2006).

(3) Climate is heterogeneous, resulting from considerable spatial variability in temperature (average annual temperature ranging from 9.4 to 30.8°C) and rainfall (average annual total precipitation up to 981 mm; both from www.worldclim.org).

(4) The limit between the Sahara and the Sahel constitutes the transition between the Palaearctic and Afro-Tropical biogeographic realms (Olson *et al.*, 2001; Holt *et al.*, 2013), resulting in latitudinal variation in species distribution and increased local biodiversity (Dumont, 1982; Le Houérou, 1992).

(5) The Sahara-Sahel spreads over ten countries, many rated as low development (UNDP, 2010) and characterised by long-term political instability (Ewi, 2010; Walther & Retaillé, 2010; Lohmann, 2011), making field surveys and trans-border research and conservation planning difficult.

(6) The onset of desert conditions in the Sahara was estimated as rather recently, at approximately 7 million years ago (Mya) in Chad (Schuster *et al.*, 2006) or around 6 to 2.5 Mya in western areas (Swezey, 2009).

(7) Perhaps most importantly, the Sahara-Sahel experienced (and is still experiencing) strong climatic oscillations, with feedback mechanisms between rainfall reduction and vegetation cover (Wang *et al.*, 2008; Claussen, 2009). Since the Pliocene (5.3 to 2.5 Mya), the Sahara-Sahel has experienced multiple dry-wet cycles (Le Houérou, 1997). The latest humid period occurred at the mid-Holocene, when the region was covered with extensive vegetation, lakes and

wetlands (Gasse, 2000; Kröpelin *et al.*, 2008). This wet period ended between 6 and 5000 years ago, when aridity greatly increased, mesic vegetation communities disappeared, and lake levels decreased (Foley *et al.*, 2003; Holmes, 2008). Such climate and land-cover oscillations have greatly shifted the Sahara-Sahel limits, further regulating biodiversity patterns (Dumont, 1982; Le Houérou, 1992, 1997; Drake *et al.*, 2011).

The dynamic Sahara-Sahel region is highly appealing for biodiversity and evolutionary research, but its large size, remoteness, and long-term political instability contributed substantially to a generalised lack of knowledge during most of the 20th century. Temporal variation on Saharan biodiversity research, tracked by the number of scientific papers published on this topic in the last 140 years, highlights that research has been highly dependent on fluctuations in the political stability of the region (Fig. 2). The relatively peaceful period experienced in the decade 2001–2010 has translated into an impressive increase in the number of studies devoted to the region, for all taxonomic groups examined. These research efforts coupled molecular and geomatic (Global Navigation Satellite Systems and Geographical Information Systems) tools together with broad sampling of taxa. Such studies are starting to unravel micro-hotspots of biodiversity and cryptic diversity, and to provide information on the causes, timing and patterns of radiation and divergence for multiple taxa. These studies are also expanding tremendously our knowledge on biodiversity distribution and evolution, but also revealing gaps on these topics in urgent need of research effort for efficient planning of biodiversity conservation. Effective management policies are required as many large-sized vertebrates have been driven to regional extinction by hunting, including birds [e.g. *Chlamydotis undulata* (Goriup, 1997); *Struthio camelus* (Thiollay, 2006)] and mammals [e.g. *Loxodonta africana* (Barnes, 1999; Bouché *et al.*, 2011); *Acinonyx jubatus* (Saleh, Helmy & Giegengack, 2001); *Oryx dammah* (Beudels *et al.*, 2005); *Panthera leo* (Barnett *et al.*, 2006)], or reduced to extremely low population sizes [e.g. *Addax nasomaculatus* and *Gazella leptoceros* (Manlius, 2000; Wacher *et al.*, 2004; Beudels *et al.*, 2005)]. The region is cyclically affected by disastrous droughts (Brooks, 2004) and, furthermore, it is predicted to experience the fastest velocities of climate change among world deserts (Loarie *et al.*, 2009), which will increase vulnerability to extinction of the already fragile biodiversity (Davies *et al.*, 2012).

The present review aims to track trends in the knowledge about biodiversity patterns and evolutionary processes across the Sahara-Sahel as well as to anticipate needs for biodiversity research and conservation. Focus is given to the most recent findings stemming from the use of molecular and geomatic tools. In particular, it aims to: (*i*) identify biogeographical patterns in the distribution of biodiversity as well as knowledge gaps on such diversity; (*ii*) emphasise the role of mountains as biodiversity refugia and of micro-scale water features as local biodiversity hotspots; (*iii*) relate palaeo-ecological events with diversification and speciation mechanisms and provide a synthetic overview of the most commonly hypothesised diversification mechanisms; (*iv*) identify present and future predicted threats to biodiversity; (*v*) evaluate gaps in biodiversity conservation targets and the main reasons for such gaps; and (*vi*) identify relevant actions for local biodiversity conservation. Finally, a set of research priorities is provided to identify the framework data needed to support regional conservation planning.

II. DISTRIBUTION OF BIODIVERSITY

Knowledge on biodiversity distribution across the Sahara-Sahel is scarce in relation to neighbouring areas (Fig. 3A). Large portions of northern-eastern Mauritania, northern Mali, western Algeria, southern Libya, and almost all mountain regions, are under-sampled. Current knowledge on species richness is particularly low in the Adrar des Ifoghas, Tibesti, Ennedi, and Marra mountains (for locations see Fig. 1), where there is scarce or non-existent sampling effort. Compilation and analysis of available species distribution data for Sahara-Sahel fauna (Dumont, 1982; Le Berre, 1989, 1990; Lévêque, 1990; Kingdon, 1997; Rödel, 2000; Denys, Granjon & Poulet, 2001; Crochet, Geniez & Ineich, 2003; Carranza *et al.*, 2004, 2008; Geniez *et al.*, 2004; Wilson & Reeder, 2005; Baha El Din, 2006; Geniez & Arnold, 2006; Johnson *et al.*, 2006; Trape & Mané, 2006; Brito *et al.*, 2008, 2010, 2011*c*; Sindaco & Jeremčenko, 2008; Arnold, Robinson & Carranza, 2009; Granjon & Duplantier, 2009; Hoath, 2009; Nicolas *et al.*, 2009; Trape, 2009; Brahmi *et al.*, 2010; African Chiroptera Report, 2011; Ferreira *et al.*, 2011; Geniez, Padial & Crochet, 2011; Hekkala *et al.*, 2011; Wagner *et al.*, 2011; Trape, Chirio & Trape, 2012) indicates the presence of a total of 305 species of dragonflies, fishes, amphibians, reptiles and mammals, distributed mainly along a series of potential corridors and refugia (Table 1). The role of mountains in deserts and arid regions as refugia now is being emphasised, and supported by studies in several taxa, such as ferns (Anthelme, Mato & Maley, 2008; Anthelme, Abdoulkader & Viane, 2011), fishes (Trape, 2009), amphibians and reptiles (Geniez & Arnold, 2006; Tellería *et al.*, 2008; Brito *et al.*, 2011*b*,*c*; Vale *et al.*, 2012*b*), birds (Tellería, 2009), and mammals (Busby *et al.*, 2009; Brito *et al.*, 2010; Vale, Álvares & Brito, 2012*a*). For instance, the Central Sahara mountains of Hoggar and Termit are major refugia for threatened large ungulates and carnivores [e.g. *Ammotragus lervia*, *Nanger dama* and *Addax nasomaculatus* (Wacher *et al.*, 2004); *Acinonyx jubatus* and *Panthera pardus* (Busby *et al.*, 2009)], most likely due to their relative inaccessibility to poachers and to generalised low human activity. Mountains host 41 Sahara-Sahel vertebrate endemics (51% of all endemics), with the Aïr (29% of all endemics), Adrar Atar (23%), and Hoggar (21%) particularly rich (see online Appendix S1), and contain isolated populations of 88 vertebrates of non-Saharan origin (45% of all non-Saharan). These isolated populations of species of non-Saharan origin persist in restricted habitats within oases and mountains of the Sahara-Sahel, suggesting temporal distribution shifts linked to Plio-Pleistocene climate

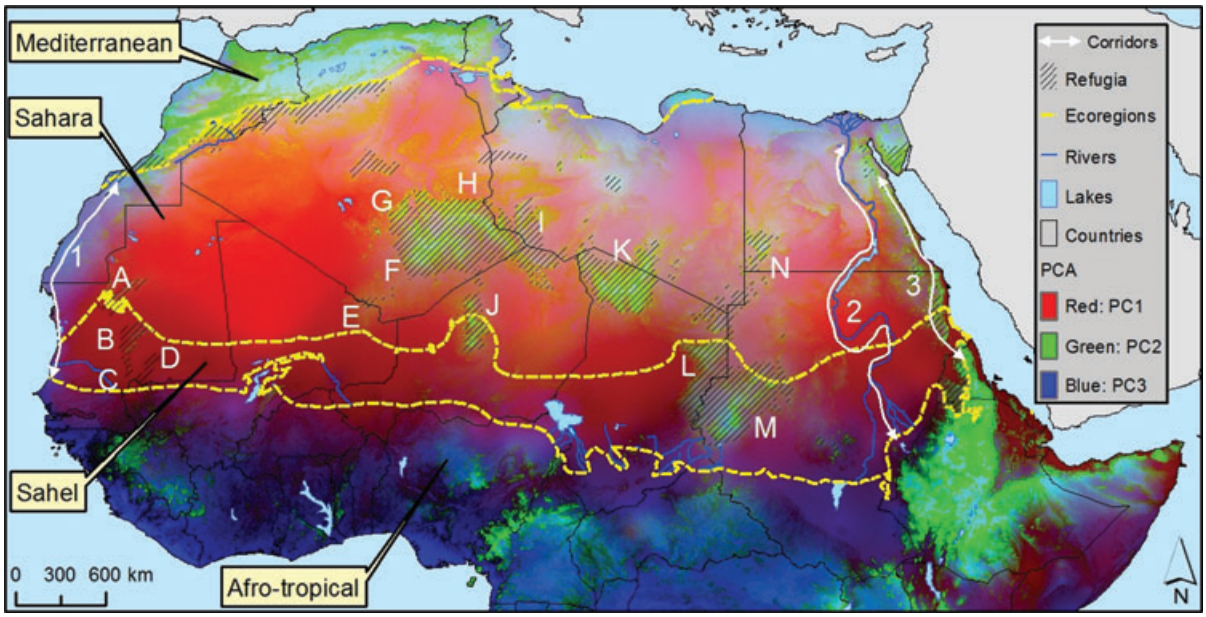

Fig. 1. Environmental variability in North Africa derived by spatial principal components analysis (SPCA), approximate boundaries between ecoregions (Olson *et al.*, 2001), and hypothesised dispersal corridors (1. Atlantic Sahara; 2. Nile River; 3. Red Sea Sahara) and refugia across the Sahara-Sahel (A, Adrar Atar-Kediet ej Jill; B: Tagant; C: Assaba; D: Afollé; E: Adrar des Ifoghas; F: Hoggar; G: Mouydir; H: Tassili n'Ajjer; I: Fezzan; J: Aïr; K: Tibesti-Dohone; L: Ennedi-Borkou; M: Marra; N: Uweinat-Gilf Kebir) (Dumont, 1982; Drake *et al.*, 2011). Composite map of SPCA, where PC1 (44.0%): annual precipitation, precipitation of wettest month, and temperature annual range; PC2 (33.4%): altitude, annual mean temperature, and minimum temperature of coldest month; and PC3 (9.4%): topography roughness index. Environmental factors from Worldclim database (www.worldclim.org) at 2.5 arc-second resolution.

fluctuations (Dumont, 1982; Le Houérou, 1992, 1997; Drake *et al.*, 2011) and/or recent translocations (Brahmi *et al.*, 2010). Although mountains are currently surrounded by sandy and rocky areas, they were probably connected by savannah-like habitats during past humid periods (Gasse, 2000; Kröpelin *et al.*, 2008), forming a net of biodiversity corridors (Fig. 1). Those corridors have been hypothesised to follow a North-South axis (Dumont, 1982; Drake *et al.*, 2011). Some seem to have persisted to the present, like the Atlantic and the Red Sea coastal areas, where high biodiversity levels (28 and 18 Sahara-Sahel vertebrate endemics and 33 and 23 vertebrates of non-Saharan origin, respectively) are related to the mild climate influenced by the proximity of the sea (Brito *et al.*, 2009, 2011*b*). The Nile River is also a permanent corridor for biodiversity, holding 35 Sahara-Sahel vertebrate endemics (44% of all endemics) and 102 vertebrates of non-Saharan origin (53% of all non-Saharan) with distributions along the river and productive riverbanks (see online Appendix S1). Despite exhibiting overall low species richness, the vast empty-quarters (unpopulated areas) and dune massifs of the Sahara are crucial refugia for threatened birds, large ungulates, and carnivores that suffered extreme declines in other regions [e.g. *Acinonyx jubatus* (Saleh *et al.*, 2001); *Addax nasomaculatus* (Beudels *et al.*, 2005); *Chlamydotis undulata* (Chammem *et al.*, 2012)].

In recent years, field surveys using modern geomatic tools and alternative sampling strategies (photo-trapping and non-invasive genetics) began increasing knowledge on species composition and distribution, such as on bacteria (e.g. Prigent *et al.*, 2005), ferns (e.g. Anthelme *et al.*, 2008, 2011), invertebrates (e.g. Lourenço & Duhem, 2007; Patiny & Michez, 2007; Ferreira *et al.*, 2011), fishes (Trape, 2009), amphibians and reptiles (e.g. Geniez & Arnold, 2006; Brito *et al.*, 2008, 2011*c*; Ibrahim, 2008), birds (e.g. Selmi & Boulinier, 2003; Gaskell, 2005; Salewski, Schmaljohann & Herremans, 2005; Tellería, 2009), and mammals (e.g. Baziz *et al.*, 2002; Wacher *et al.*, 2002; Padial & Ibáñez, 2005; Londei, 2008; Tellería *et al.*, 2008; Brito *et al.*, 2010; Gaubert *et al.*, 2012), as well as of migrant birds crossing the Sahara-Sahel (e.g. Meyburg *et al.*, 2004; Salewski, Schmaljohann & Liechti, 2010; Ozarowska, Stepniewska & Ibrahim, 2011) and particularly of secretive fauna [e.g. *Acinonyx jubatus* (Saleh *et al.*, 2001; Hamdine, Meftah & Sehki, 2003); *Panthera pardus* (Busby *et al.*, 2009); bats (Rebelo & Brito, 2007)]. Phylogeographic studies using molecular markers are also uncovering cryptic diversity [e.g. *Apis mellifera* (El Niweiri & Moritz, 2008; Shaibi *et al.*, 2009); *Acanthodactylus* spp. (Fonseca *et al.*, 2008); *Ptyodactylus* spp. (Froufe *et al.*, 2013)] and, in some cases, splitting previously considered wide-ranging species, including multiple invertebrates [e.g. *Cataglyphis* spp. (Knaden *et al.*, 2005); *Hottentotta* spp. (Sousa *et al.*, 2011)], reptiles [e.g. *Chalcides* spp. and *Sphenops* spp. (Carranza *et al.*, 2008); *Agama* spp. (Geniez *et al.*, 2011); *Crocodylus* spp. (Hekkala *et al.*, 2011); *Trapelus* spp. (Wagner *et al.*, 2011)], and mammals [e.g. *Taterillus* spp. (Dobigny *et al.*, 2005); *Acomys* spp. (Volobouev *et al.*, 2007; Frynta *et al.*, 2010);

Table 1. Species richness of endemic and relict taxa (combining dragonflies, fishes, amphibians, reptiles, and mammals) in hypothesised dispersal corridors and refugia of the Sahara-Sahel region

	Biogeographic range of species					
	AFT	SHL	SAH	SAS	MED	**Total**
Corridors:						
Atlantic Sahara	16	9	19	12	18	74
Nile River	108	5	30	18	7	168
Red Sea Sahara	23 (30)	4 (3)	14 (0)	20 (3)	3 (0)	64 (36)
Refugia:						
Adrar Atar - Kediet ej Jill	20	6	12	10	1	49
Tagant	32	3	6	4	0	45
Assaba	25	2	3	0	0	30
Afollé	11	1	4	1	0	17
Adrar des Ifoghas	19	6	7	5	1	38
Hoggar	10	3	14	15	6	48
Mouydir	10	0	6	6	1	23
Tassili n′Ajjer	12	1	13	9	3	38
Fezzan	4	1	10	7	4	26
Aïr	39	12	11	11	3	76
Tibesti - Dohone	13	4	6	6	1	30
Ennedi-Borkou	23	5	5	3	1	37
Marra	17	3	0	1	0	21
Uweinat-Gilf Kebir	4	0	4	5	0	13
Total numberof individual species	168	20	60	31	26	305

Location of corridors and refugia are indicated in Fig. 1. Richness is presented according to biogeographic range of species: Afro-tropical (AFT), Sahelian endemic (SHL), Saharan endemic (SAH), Saharo-Sindian (SAS), Mediterranean (MED). Values in parenthesis include species present in the Red Sea Sahara corridor that are distributed south of Gebel Elba, thus not entering the Sahara. Detailed data for each taxonomic group are provided as supporting information in online Appendix S1.

Jaculus spp. (Ben Faleh *et al.*, 2010, 2012; Boratyński, Brito & Mappes, 2012)]. Such studies are changing completely perceptions on regional biodiversity patterns. Instead of relatively low species diversity with distribution covering most of the region, broad taxa sampling and use of molecular tools suggest a larger number of species with much narrower ranges, frequently limited to micro-hotspots of biodiversity. At the same time, such studies are stressing that present knowledge on biodiversity distribution is incomplete. In fact, only a few comprehensive and recent distribution atlases are available, mostly biased towards amphibians and reptiles (e.g. Geniez *et al.*, 2004; Trape & Mané, 2006; Trape *et al.*, 2012), which hampers the identification of regional biodiversity hotspots. As such, observational data collected at high spatial resolution (less than 1 km) are forming the basis of ecological niche-based models (Fig. 3B) that allow estimation of habitat suitability for elusive species distributed across remote areas, such as canids and vipers (Brito *et al.*, 2009, 2011*b*). Despite exhibiting wide extents of occurrence, from the Atlantic to the coasts of the Red Sea, fine-scaled ecological niche models suggest much smaller areas of occupancy, in rather fragmented distributions, and adaptation to particular habitats or environmental extremes [e.g. *Vulpes rueppellii* and *V. zerda* (Brito *et al.*, 2009); *Cerastes cerastes* and *C. vipera* (Brito *et al.*, 2011*b*)]. Ecological niche modelling of Sahel mountain endemics has also identified restricted and relatively fragmented suitable habitats for some of these species [e.g. *Felovia vae* (Vale *et al.*, 2012*a*); *Agama boulengeri* (Vale *et al.*, 2012*b*)]. Such models indicate that annual precipitation, precipitation of wettest month, and temperature annual range account for most of the environmental variation within the range of the Sahara-Sahel vertebrates (Fig. 1), and geographical variation in rainfall and temperature are major factors related to the biodiversity distribution of vegetation (El-Ghani, 1998), invertebrates (Patiny *et al.*, 2009), reptiles (Brito *et al.*, 2011*b*; Vale *et al.*, 2012*b*), and mammals (Brito *et al.*, 2009; Nyári, Peterson & Rathbun, 2010; Vale *et al.*, 2012*a*), and human-related factors in threatened birds (Chammem *et al.*, 2012).

Within the Sahara-Sahel, high concentrations of species are found around waterbodies (Rebelo & Brito, 2007; Trape, 2009; Brito *et al.*, 2011*c*), giving these features the status of micro-hotspots of biodiversity. Oases in sand-seas are crucial for humans but also constitute refugia for multiple species (particularly to fishes and amphibians within vertebrates) around the most extreme arid areas of the Sahara (Le Berre, 1989, 1990; Saleh *et al.*, 2001; Selmi & Boulinier, 2003; Brito *et al.*, 2008). Recent studies in Mauritania are also emphasising the conservation importance of mountain lagoons (locally known as *gueltas*) that hold endemic fauna and range-margin populations (Fig. 4A). These pools are sparsely distributed in temporal riverbeds in mountains surrounded by sandy areas and allow the maintenance of rich communities, acting as refugia to relict populations and potential speciation drivers (Anthelme *et al.*, 2008). Isolated populations of tropical and endemic species can be

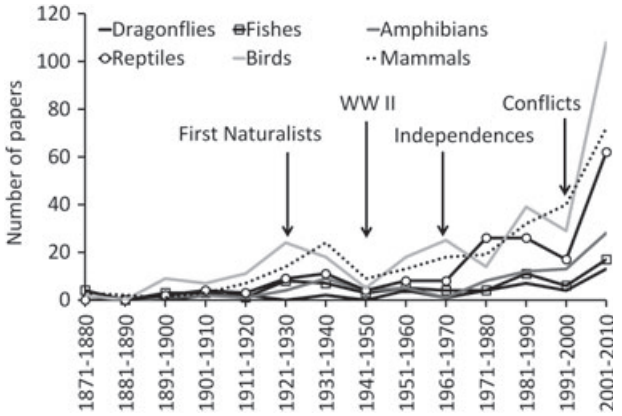

Fig. 2. Decadal evolution of the number of papers listed in *Zoological Records* since 1871 with the key word 'Sahara' and corresponding animal group. Historical events that shaped the temporal evolution of the number of papers are also identified. Until the early 20th century, the Sahara was kept off bounds to research. The first naturalists surveyed the area, following the military conquest of Saharan territories, until World War II. Afterwards, research effort fluctuated according to human conflicts in the region: there were significant research increases after the 1950s, and noticeable collapses after independence from European administration, and during a series of conflicts that erupted throughout many countries (e.g. Tuareg rebellion in the Central Sahara). The 21st century saw a burst of research that translates into an unprecedented number of published papers.

found in *gueltas*, including dragonflies [e.g. *Ischnura saharensis*, *Trithemis annulata* (Dumont, 1982; Ferreira *et al.*, 2011)], fishes [e.g. *Barbus macrops*, *Clarias anguillaris* (Trape, 2009)], amphibians [e.g. *Hoplobatrachus occipitalis*, *Amietophrynus xeros* (Tellería, 2009)], reptiles [e.g. *Crocodylus suchus*, *Ptyodactylus ragazzi*, *Python sebae*, *Varanus niloticus* (Brito *et al.*, 2011*b*)], birds [e.g. *Burhinus senegalensis*, *Hieraaetus spilogaster* (Tellería, 2009)], and mammals [e.g. *Felovia vae*, *Procavia capensis*, *Papio papio* (Brito *et al.*, 2010).

The occurrence of crocodiles (*Crocodylus suchus*) in Saharan *gueltas* constitutes a spectacular example of the value of refugia for relict tropical fauna. Extirpated from Morocco and Algeria in the first half of the last century, a few relict populations were known to persist in Chad and Mauritania (Brito *et al.*, 2011*c*). Field surveys conducted in Mauritania recently updated their distribution and habitat selection, finding that *gueltas* were the most frequent waterbody used by crocodiles and that most *gueltas* had less than five adults (Brito *et al.*, 2011*c*). There is evidence of individual dispersal between some water localities (usually located at an average distance of less than 4 km) that may attenuate loss of genetic diversity in *gueltas*. Dispersal may occur during the rainy season, when raging water fills streams and partially connects *gueltas* and mountain lagoons, and occasionally mountains with the Senegal River. Remote sensing techniques quantifying hydrological features of central-southern Mauritania have detected distinct water availability patterns (Campos, Sillero & Brito, 2012) that may relate to dispersal events. Molecular markers are needed to quantify population sub-structuring and effective population size, and to detect the occurrence of gene flow.

III. EVOLUTION OF BIODIVERSITY

Phylogeographic studies are revealing that diversification and speciation events that occurred in the Sahara-Sahel are most likely related to temporal and spatial variation of desert extent. The onset of the Sahara presumably acted mainly as a North-South vicariant feature, being associated with diversification processes for several species (Carranza *et al.*, 2002, 2008; Carranza, Arnold & Pleguezuelos, 2006; Geniez & Arnold, 2006; Wagner *et al.*, 2011; Metallinou *et al.*, 2012) and to allopatric effects (Douady *et al.*, 2003; Muwanika *et al.*, 2003; Pook *et al.*, 2009; Gonçalves *et al.*, 2012). The palaeoclimatic oscillations following Sahara formation are estimated to have occurred at cycles of approximately 100000–20000 years during the last million years (Le Houérou, 1997), which greatly shaped the range of desert and savannah environments and constrained species distribution (Dumont, 1982; Le Houérou, 1992, 1997; Drake *et al.*, 2011) and genetic structure (Fig. 5). For example, independent approaches using molecular markers and ecological niche-based modelling suggest vicariance as the major diversification force for the origin of the small mammal *Elephantulus rozeti*, which was linked to post-Pleistocene allopatry induced by increasing aridity in the Sahara (Douady *et al.*, 2003; Nyári *et al.*, 2010).

Assuming a neutral scenario (without adaptation processes) as the main driver of speciation in the Sahara-Sahel, divergence within species occurred through vicariant events, where allopatric effects induced the interruption of gene flow and led to evolutionarily independent lineages or new species. The time and nature of vicariant events have variable effects on taxa according to their habitat requirements (Fig. 6). Xeric species likely experienced diversification processes during humid periods [e.g. *Tarentola* spp., *Chalcides* spp. and *Sphenops* spp. (Carranza *et al.*, 2002, 2008); *Jaculus* spp. (Boratyński *et al.*, 2012); *Stenodactylus* spp. (Metallinou *et al.*, 2012)]. Conversely, population contraction and diversification events under hyper-arid conditions likely occurred in multiple mesic vertebrates, adapted to arid conditions but still requiring some moisture [e.g. *Taterillus* spp. (Dobigny *et al.*, 2005); *Malpolon* spp. and *Hemorrhois hippocrepis* (Carranza *et al.*, 2006); *Pristurus* spp. (Geniez & Arnold, 2006); *Psammophis* spp. (Rato *et al.*, 2007); *Galerida* spp. (Guillaumet, Crochet & Pons, 2008); *Acomys* spp. (Nicolas *et al.*, 2009); *Rhabdomys dilectus* (Castiglia *et al.*, 2012); *Agama* spp. (Gonçalves *et al.*, 2012); *Gazella* spp. (Godinho *et al.*, 2012)]. The ancestors of these species most likely entered the region during wet periods and diversified during the arid phases of the Plio-Pleistocene. During these arid periods, mesic species suffered range fragmentation in wetter and milder areas, such as rocky massifs and mountain ranges. Recent population expansions have been observed for mesic taxa during humid periods

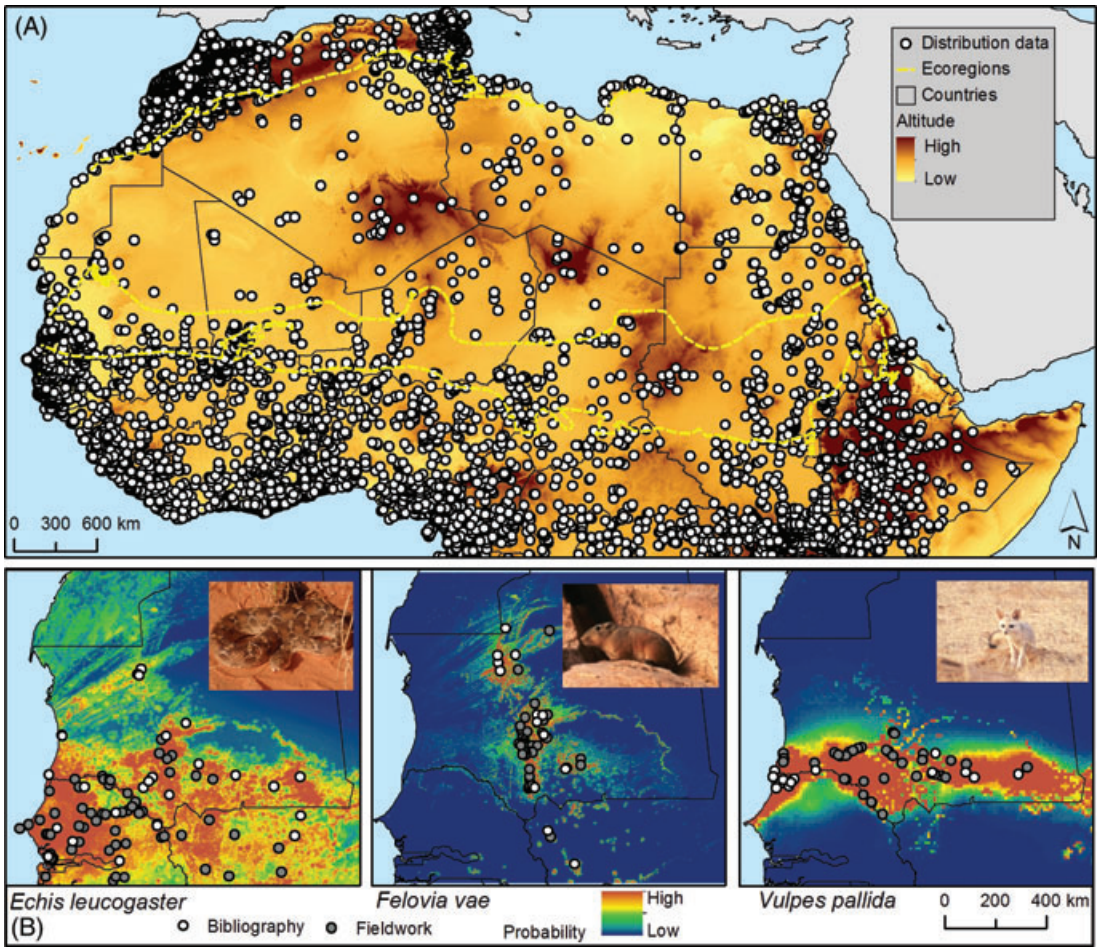

Fig. 3. (A) Distribution data available for vertebrates in North Africa at the Global Biodiversity Information Facility (GBIF, 2012). (B) Examples of increasing knowledge on distribution and habitat suitability in the west Sahara-Sahel region for range-margin populations of Afro-tropical taxa (*Echis leucogaster*), local endemic taxa (*Felovia vae*) and Sahelian-endemic taxa (*Vulpes pallida*). Suitability maps are derived from ecological niche-based models and represent presence probability. Known occurrence localities are represented as data published mainly before the year 2000 (bibliography) and fieldwork data collected after the year 2000 to develop models (fieldwork). Distribution data and suitability maps for *E. leucogaster*, *F. vae* and *V. pallida* adapted from Brito *et al.* (2011*b*); Vale *et al.* (2012*a*), and Brito *et al.* (2009), respectively.

(Froufe, Brito & Harris, 2009). Divergence events occurred during hyper-arid periods particularly for water-dependent species: during wet periods, these species occur continuously along permanent or temporary rivers, and become extinct or isolated in small waterbodies (oases and *gueltas*) during dry periods [e.g. *Mastomys huberti* (Mouline *et al.*, 2008); *Astatotilapia desfontainii* (Genner & Haesler, 2010); *Apis mellifera* (Shaibi & Moritz, 2010)]. Similar vicariant patterns are suggested for taxa that show divergence processes by isolation into savannah patches during Plio-Pleistocene climatic shifts, with recent demographic expansions occurring during arid phases since the Holocene [e.g. *Mastomys erythroleucus* (Brouat *et al.*, 2009)]. Climatic fluctuations also led to changes in hydrological networks that affected major river courses and might prompt vicariant processes, as suggested in Lake Chad and in the Nile River (Dobigny *et al.*, 2005; Hassanin *et al.*, 2007; Brouat *et al.*, 2009; Pook *et al.*, 2009). Existing molecular studies have mostly focused on non-volant small vertebrates with relatively low dispersal capacity and for which barrier effects may be more pronounced. The few studies available on highly mobile vertebrate species show little geographic genetic structure in all North Africa [e.g. *Gazella dorcas* (Lerp *et al.*, 2011); *Canis* spp. (Gaubert *et al.*, 2012).

The cycles of population expansion during favourable climatic conditions and population contraction with harsh climate translated into opposing patterns: (*i*) dispersal along the geographical corridors that facilitated gene flow during suitable climatic periods [e.g. *Canis* spp. (Gaubert *et al.*, 2012)]; (*ii*) divergence without gene flow in refugia and promotion of speciation [e.g. *Taterillus* spp. (Dobigny *et al.*, 2005)] and morphological evolution [e.g. *Galerida* spp. (Guillaumet *et al.*, 2008)] during unsuitable climatic periods. Mountains play a key role in diversification patterns across the Sahara-Sahel by acting as refugia for many species and facilitating gene flow during favourable climatic conditions. Thus, harsh climatic conditions allowed divergence of

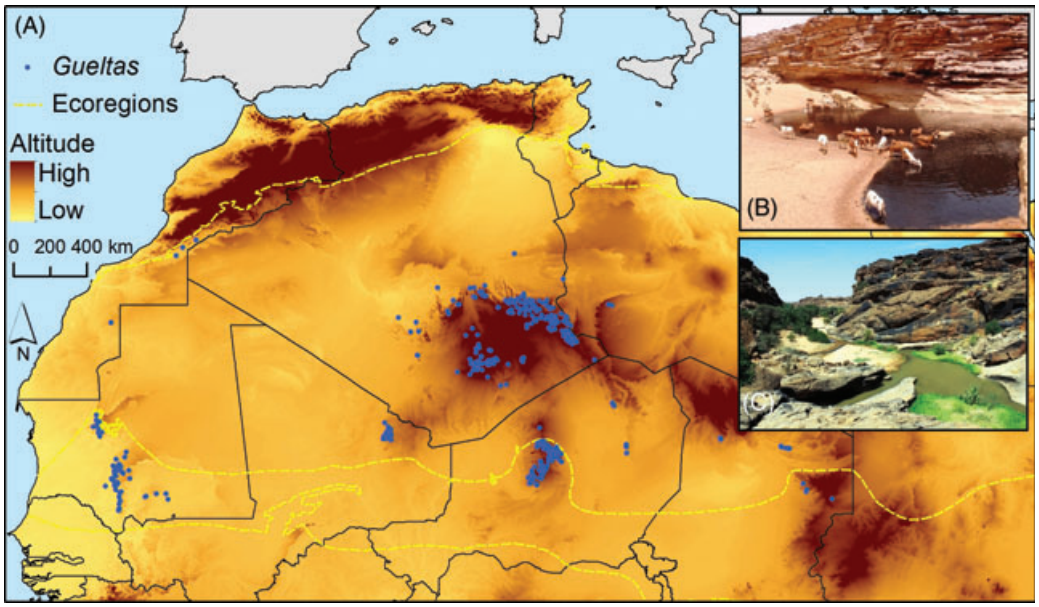

Fig. 4. (A) Distribution of rock pools (*gueltas*) in the Sahara-Sahel. *Gueltas* are mostly concentrated in mountains. Coordinates of *gueltas* manually collected from fieldwork (Campos *et al.*, 2012) and topographic maps (Institut Géographique National, Paris; 1:200,000 series). (B, C) Insights of heavily exploited and eutrophicated *guelta* El Khedia (B) and pristine *guelta* Metraoucha (C), Mauritania, both holding isolated crocodile populations (Brito *et al.*, 2011*c*).

multiple taxa in mountains, possibly resulting in long-term allopatric isolation and speciation [e.g. *Agama tassiliensis* (Geniez *et al.*, 2011; Gonçalves *et al.*, 2012]. On the other hand, mountain populations have likely been at the origin of several episodes of expansion, promoting gene flow events between isolated populations [e.g. *Olea* spp. (Besnard, Rubio de Casas & Vargas, 2007); *Myrtus* spp. (Migliore *et al.*, 2012)]. For instance, Central Saharan mountains harbour a variety of Mediterranean-origin plant species that have been able to survive long-distance colonisation episodes and now constitute relict populations of great conservation interest [e.g. *Senecio* spp. (Coleman *et al.*, 2003); *Atriplex* spp. (Ortíz-Dorba *et al.*, 2005); *Myrtus* spp. (Migliore *et al.*, 2012)]. Ecological adaptation and morphological convergence have been reported in contact zones of lizards [e.g. *Acanthodactylus* (Crochet *et al.*, 2003)], but molecular studies are needed to understand patterns of gene flow dynamics.

At the same time, organisms inhabiting the Sahara-Sahel have developed unique adaptive features to cope with the harsh environmental conditions, including unpredictable and limited water and food resources, and extreme temperatures and solar radiation. Most desert-dwellers avoid exposure or activity during the hottest parts of the day (mid-day) and year (dry season). Some evolved larger body size to avoid over-heating by increased thermal inertia (when evaporative cooling is not possible) that allows activity during daylight [e.g. *Psammomys obesus* (Haim, Alma & Neuman, 2006)]. An elongated body, wedge-shaped head and limb reduction evolved multiple times in 'grass swimmers' and 'sand burrowers' [e.g. *Chalcides* spp. and *Sphenops* spp. (Carranza *et al.*, 2008); *Scincus scincus* (Maladen *et al.*, 2009)]; these are examples of complex and unique adaptations to dry habitats that increase mobility under sand and grass in savannah and desert conditions. Two other important physiological adaptations are connected with limited food and water resources. Reduced resting metabolic rate evolved multiple times (e.g. *Acomys russatus*, *Lepus capensis*, Bedouin goat) in response to selective pressures, allowing more efficient conservation of energy and water (Choshniak *et al.*, 1996; Kronfeld & Shkolnik, 1996). Reduction of overall energy turnover, as well as lower metabolic rate, is connected with another physiologically adaptive mechanism: long retention time of fluid in the gastrointestinal tract. Such water-saving mechanisms allowed species to survive and persist even in an environment without permanent, or indeed any, water resources, such as the vast empty quarters of the Sahara desert [e.g. *Addax nasomaculatus* (Hummel *et al.*, 2008); *Lepus capensis* (Kronfeld & Shkolnik, 1996)].

IV. THREATS TO BIODIVERSITY AND CONSERVATION PLANNING

Biodiversity in the Sahara-Sahel is presently under threat as a direct result of the synergistic effects of climate change, habitat alteration and most notably, the effect of other multiple human pressures. The spreading of four-wheel-drive vehicles and firearms from the beginning of the 20th century increased dramatically the extent and impact of hunting activities (Valverde, 1957; Newby, 1980), resulting in local extinction of large mammals [e.g. *Giraffa camelopardalis* (Ciofolo, 1995); *Acinonyx jubatus* (Saleh *et al.*, 2001); *Oryx dammah* (Beudels *et al.*, 2005); *Panthera leo* (Barnett *et al.*, 2006)]

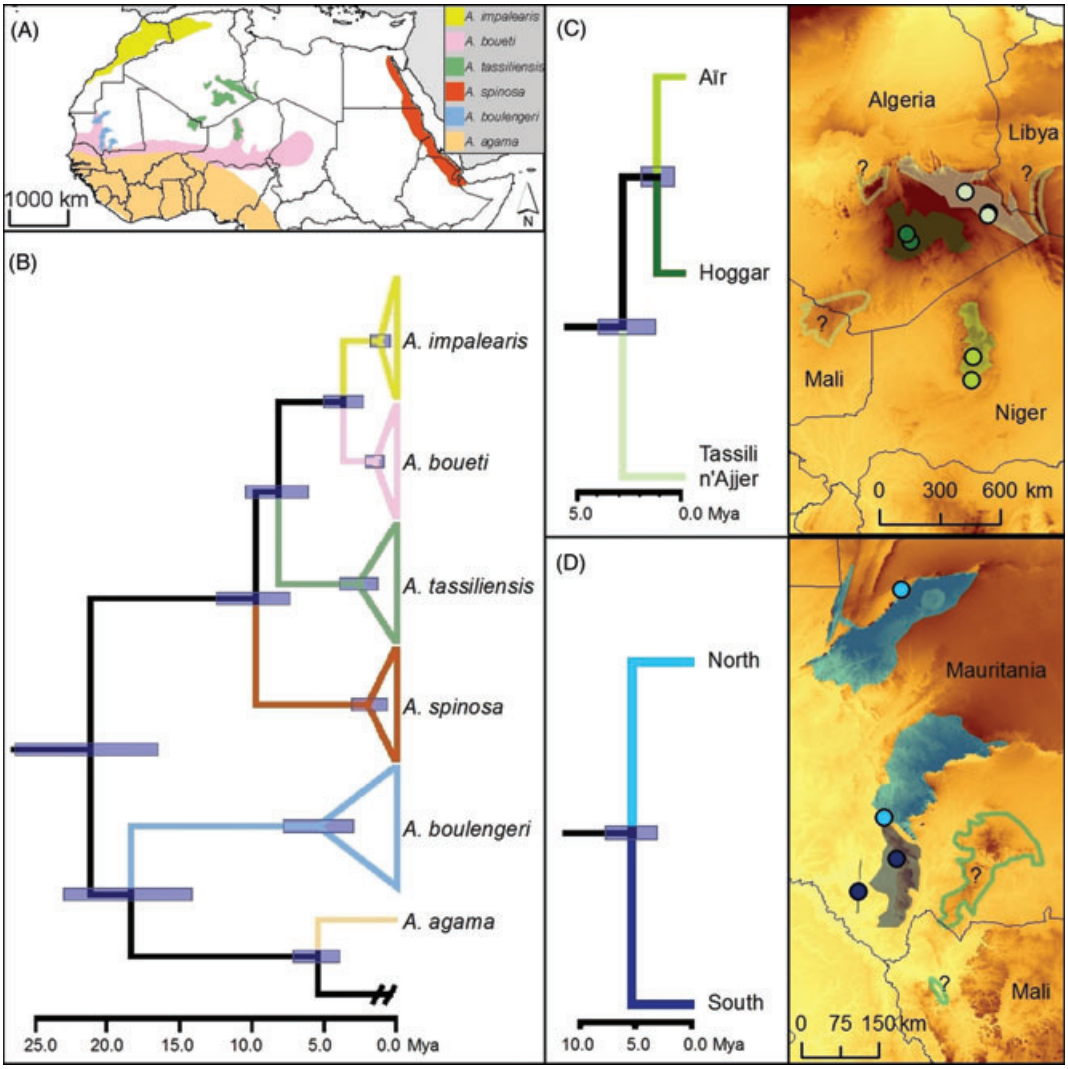

Fig. 5. (A) Distribution and (B) phylogenetic relationships of North African *Agama* lizard species. Detailed biogeographic patterns of mountain endemic lineages of (C) *A. tassiliensis* in Central Sahara and of (D) *A. boulengeri* in West Sahara-Sahel (colour scale on maps indicates elevation). Colours identify species and lineages within species; polygons in A delimit approximate distributions of lineages; in C and D question marks show genetically undefined populations and dots represent sequenced specimens. Shaded horizontal bars in the phylogenetic tree correspond to estimates of diversification times (with confidence intervals) for *Agama* lineages, with a scale bar denoting millions of years ago (Mya). Data adapted from Gonçalves *et al.* (2012).

and birds [e.g. *Chlamydotis undulata* (Goriup, 1997); *Struthio camelus* (Ostrowski, Massalatchi & Mamane, 2001; Thiollay, 2006)]. Conflicts related to water accessibility have resulted in the extinction of relict crocodile populations throughout the Sahara-Sahel (Brito *et al.*, 2011*a*,*c*). Overgrazing, wood collection and conversion of natural habitats into pastures and agricultural fields have also affected large portions of the Sahel by fragmentation and destruction of savannah-like micro-habitats (ECOWAS & SWAC-OCDE, 2006). More recently, the extraction of natural resources (oil, gas and mining) has become widespread over the Sahara (Fig. 7), and prospection for new oil sources has increased over the last decade, endangering the last known viable addax (*Addax nasomaculatus*) populations in Niger (Rabeil, 2011). The escalating conflict observed in the Sahel since 2012 is also prompting disastrous declines in endangered ungulates across the Sahara-Sahel (Zedany & Al-Kich, 2013) and is likely threatening the northernmost population of elephants (*Loxodonta africana*) in Africa, located in the Sahel of Mali and Burkina-Faso (Wall *et al.*, 2013).

Mountain lagoons are important for humans, providing water for both human and cattle consumption (Fig. 4B). Water overexploitation produces several conservation problems, including shortage during the dry season, faecal contamination, excessive eutrophication, and increased activities for excavating pools or pumping water (Tellería *et al.*, 2008; Brito *et al.*, 2011*c*). Moreover, documented reductions in water-dependent species diversity and population sizes (Jödicke *et al.*, 2004; Trape, 2009; Brito *et al.*, 2011*c*) as a direct consequence of the dramatic droughts in the

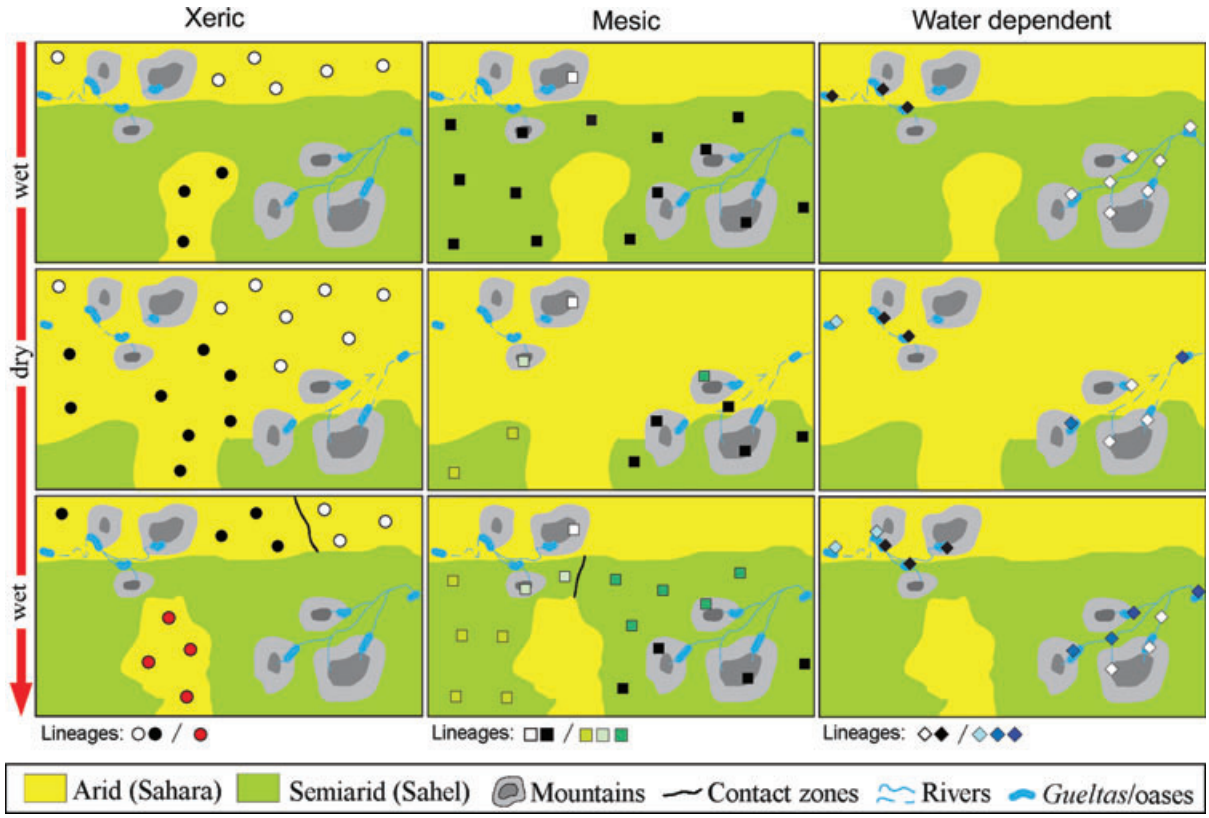

Fig. 6. Summary of hypothetical diversification mechanisms through allopatric processes expected for three types of Saharan-adapted species: xeric (circles), mesic (squares) and water-dependent species (diamonds). A time series of climatic cycles is shown from top to bottom. Wet periods associated with a cooler climate lead to expansion of semiarid environments (Sahel) while dry periods, associated with a warmer climate, lead to wider arid environments (Sahara). Cycles of range expansion-contraction lead to the formation of new lineages (colours) and subsequent contact zones between lineages (black lines).

1970s (Brooks, 2004) suggest a major threat for biodiversity at *gueltas* under predicted global warming scenarios.

New threats for biodiversity are forecasted with global climate warming at an unprecedented rate in the last 1000 years (IPCC, 2007). North Africa is a land of extremes, being traditionally affected by climate fluctuations (Foley *et al.*, 2003; Claussen, 2009). During the 20th century, Africa warmed by 0.5°C (Hulme *et al.*, 2001) and predictions of human-induced climate change for the continent suggest that this warming will continue, especially in desert biomes, where the predicted rate of temperature increase is highest (Hulme *et al.*, 2001; Loarie *et al.*, 2009). Future climate warming is likely to affect the phenology, physiology and distribution of many species and the synergistic combination with other human-induced habitat fragmentation and loss will likely increase range contraction and species extinction (Pimm, 2008). Ecological niche-based models are forming the basis for simulating future distributions under climate-change scenarios. Predictions for migrant passerines and breeding birds indicate extensive range contractions and species loss across the Sahel and the northern margin of the Sahara, respectively (Barbet-Massin *et al.*, 2009; Barbet-Massin, Thuiller & Jiguet, 2010). Protected areas located in deserts and xeric shrublands are expected to suffer dramatic losses of suitable climates for African mammals; for instance, the Tassili n'Ajjer National Park of Algeria is predicted to lose about 50% of current mammal richness with only about 10% species gain (Thuiller *et al.*, 2006). Quantifications of species range shifts and population trends in the region are mostly absent, but the few studies available reported negative population trends and range shifts constrained by the ecophysiological traits of species. Examples come from multiple taxonomic levels, such as woody vegetation (Wezel, 2005; González, Tucker & Sy, 2012), fishes (Trape, 2009), reptiles (Brito *et al.*, 2011*c*), and small mammals (Thiam, Bâ & Duplantier, 2008). By contrast, invasion of alien species profiting from agricultural expansion associated with human settlements has been reported (Bachir *et al.*, 2011). Regional red-listing is mostly unavailable for all taxonomic groups and countries within the Sahara-Sahel, with the exception of Morocco where 31 and 14% of amphibians and reptiles, respectively, were identified as threatened mostly related to small species range and habitat specialisation (Pleguezuelos *et al.*, 2010). Area prioritisation for biodiversity conservation is mostly unavailable, with the exception of African dragonflies (Simaka *et al.*, 2013) and the amphibians and reptiles of Morocco (de Pous *et al.*, 2011). Both works suggest the expansion of the present conservation area network to

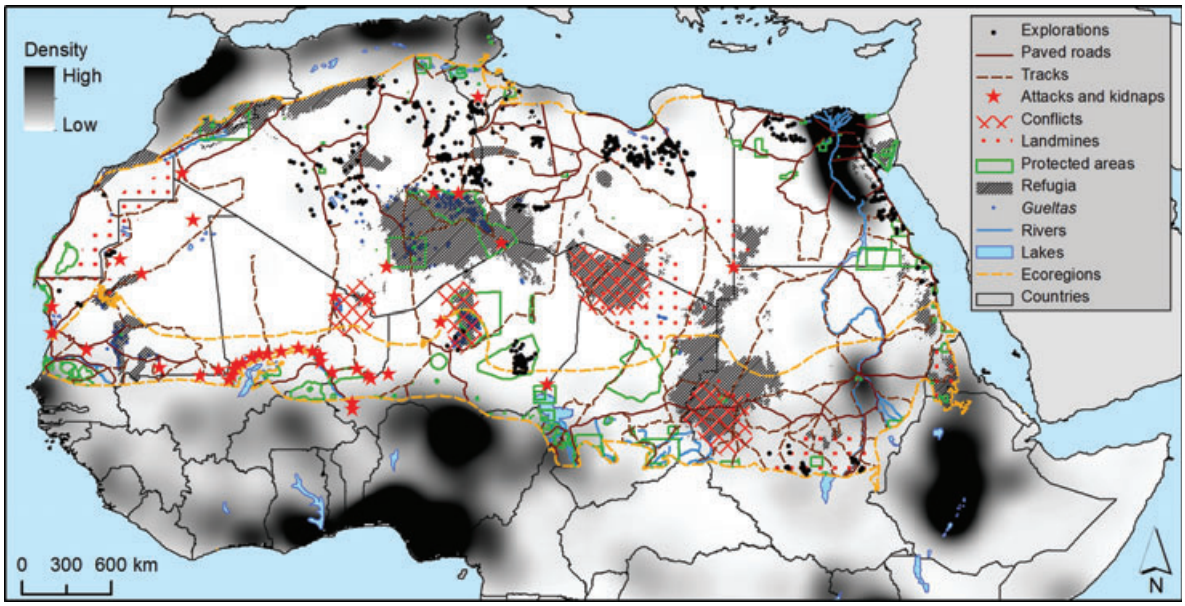

Fig. 7. Human activities in the Sahara-Sahel. Interpolated distribution of human population density in North Africa (adapted from CIESIN-FAO-CIAT, 2005), areas of insecurity including attacks on people and infrastructures and kidnapping for ransom since 2003, regions of long-standing conflict, and regions with landmine occurrence (updated from Ewi, 2010; Walther & Retaillé, 2010; www.sahara-overland.com; and www.desert-info.ch/desert-info-forum/viewtopic.php?t = 1927), areas of exploration of natural resources including gas, oil, and mining (adapted from multiple internet-based sources; e.g. Rabeil, 2011), major roads and tracks (updated from ESRI, 1996), protected areas (adapted from IUCN and UNEP, 2009), and hypothesised biodiversity refugia in the Sahara-Sahel region.

Sahara environments to ensure species persistence, even if considering low representation of species distributions across protected areas.

Whereas the Sahara-Sahel harbours several endemics, relict populations, and cryptic diversity, and supplies important ecosystem services, its conservation has been mostly neglected (UNEP, 2006; Davies *et al.*, 2012; Durant *et al.*, 2012). In fact, a small number of studies have been devoted to Sahara-Sahel biodiversity compared to other regions (Durant *et al.*, 2012), resulting in a lack of knowledge on biodiversity distribution. As such, protected area coverage in the region (7.4%; Fig. 7) is below the 10% target of the Convention on Biological Diversity (Secretariat of the Convention on Biological Diversity, 2010). The paucity of conservation actions derives from inefficiency in attracting conservation funds, probably caused by: (*i*) funding priority been given to global biodiversity hotspots (Durant *et al.*, 2012); (*ii*) generalised lack of knowledge on biodiversity distribution deriving from the remoteness of the region, regional widespread conflicts (Fig. 7), or persistent regional insecurity (Ewi, 2010; Walther & Retaillé, 2010; Lohmann, 2011); and (*iii*) chronic poverty with some countries ranking low on the human development rating (UNDP, 2010). Such limitations have resulted in conflicts between biodiversity conservation and poverty reduction (Adams *et al.*, 2004; Davies *et al.*, 2012).

The future of Sahara-Sahel biodiversity is highly dependent on the development of human societies. In this context, greater regional investment, both in human development and biodiversity conservation is needed. Resource allocation *via* major international funding institutions, such as the World Bank (www.worldbank.org) or the Global Environmental Fund (www.globalenvironmentfund.com), is paramount. In parallel and at smaller scales, non-governmental organisations and international cooperation agencies are developing biodiversity surveys and promoting the establishment of local protected areas (e.g. Cooper *et al.*, 2006). Several organisations, such as the Sahara Conservation Fund (SCF, www.saharaconservation.org), are promoting reintroductions and population monitoring of endangered ungulates (*Oryx dammah*, *Addax nasomaculatus*, and *Nanger dama mhorr*) in Algeria, Chad, Niger, Senegal and Tunisia (e.g. Abáigar *et al.*, 1997), and in 2012 the SCF promoted the creation of the largest African protected area in the Termit and Tin-Toumma of Niger. Other relevant local protected areas recently established include the reintroduction facilities for ungulates of Safia (Morocco), which are vital for maintaining overall genetic diversity of endangered ungulates (Godinho *et al.*, 2012). By contrast, the subspecies *Giraffa camelopardalis peralta* needs urgent inclusion in captive breeding programmes as it is known only from a small wild population of less than 200 individuals in Niger (Hassanin *et al.*, 2007). Community-based natural resources management policies are needed to assure human welfare with coexisting biodiversity, similarly to other successful experiences across Africa (e.g. Virtanen, 2003). Local practices and beliefs towards large vertebrates dictate levels of human persecution, and

have major implications in local extinctions or in the acceptance of *in-situ* conservation efforts (Ostrowski *et al.*, 2001; Beudels *et al.*, 2005; Brito *et al.*, 2011*a*). Local communities have an accurate perception of surrounding biodiversity (Hammiche & Maiza, 2006), revealing traditional knowledge as a useful conservation tool to determine the distribution, status and biological traits of elusive and rare species living in remote areas (Burbidge *et al.*, 1988; Kowalski & Kowalska, 1991; Brito *et al.*, 2011*a*). As such, the declaration of the Gabbou hydrological network of Mauritania as a Ramsar site (Tellería, 2009) is especially relevant, as it could generate alternative income sources for local human populations linked to birdwatching and to the presence of relict crocodile populations (Brito *et al.*, 2011*c*). Eco-tourism programmes established in protected areas, combining wildlife observation and discovery of human cultural heritage and rock art, may also be of direct benefit locally (UNEP, 2006).

V. RESEARCH NEEDS

Current research is allowing us to unravel the patterns and processes behind Sahara-Sahel biodiversity, but many questions remain unanswered, hampering regional conservation planning. The main issues in need of addressing are:

(1) Raw distribution data with GPS resolution is being collected (e.g. Brito *et al.*, 2008, 2010; Ferreira *et al.*, 2011) and high-resolution maps of suitable habitats are being produced for some taxonomic groups and regions (e.g. El-Ghani, 1998; Brito *et al.*, 2009, 2011*b*; Vale *et al.*, 2012*a*,*b*). However, there are still huge information gaps on local species richness and individual species' ranges at all taxonomic levels, and biodiversity mapping needs to be extended to many taxa, with priority given to endangered species, mountain-endemic fauna, and relict populations of non-Saharan origin. Accurate distribution data are paramount for developing atlases of biodiversity distribution. Assessments are needed in remote and hard-to-sample mountain areas, which most likely still hold undescribed endemic diversity. Environmental factors have been related to ranges of multiple vertebrates, but vulnerability and potential adaptation to climate change is still poorly understood. Remote sensing can provide environmental data appropriate to derive ecological models with high spatial and temporal resolution (e.g. Campos *et al.*, 2012).

(2) Cryptic diversity and geographic structuring in genetic diversity have been observed in widespread species (e.g. Boratyński *et al.*, 2012; Gaubert *et al.*, 2012; Gonçalves *et al.*, 2012), but the systematic status of these genetic demes and the evolutionary drivers of such diversity are mostly unknown. Molecular studies will likely continue to reveal biodiversity and genetic analysis of museum specimens will provide essential material from regions where sampling is currently nearly impossible due to political instability.

(3) Geological and palaeoclimatic events are thought to be major drivers of biodiversity (e.g. Carranza *et al.*, 2002, 2006; Geniez & Arnold, 2006; Wagner *et al.*, 2011; Metallinou *et al.*, 2012). Although the climate-driven speciation hypothesis has been suggested to explain the evolutionary patterns at interspecific and intraspecific levels in the Sahara-Sahel (e.g. Carranza *et al.*, 2002, 2008; Boratyński *et al.*, 2012; Gonçalves *et al.*, 2012), it still requires detailed verification. Integrative studies of historical biogeography, combining ecological niche modelling (e.g. Nyári *et al.*, 2010), genetic analyses and functional experiments, are needed to estimate ecophysiological (and adaptive) limits of species/clades to reconstruct and predict evolutionary trajectories, as well as to test if diversification patterns match past wide-impact events. Also, parapatric and sympatric speciation mechanisms are rarely considered and their ecological components, like character displacement hypotheses (interspecific competition), need exploration.

(4) Mountains are being emphasised as biodiversity hotspots (e.g. Trape, 2009; Brito *et al.*, 2010, 2011*b*,*c*; Geniez *et al.*, 2011), but they remain largely unexplored. The development of phylogenetic, phylogeographic and population genetic studies will most likely unravel a unique situation where the combination of long-term persistent populations with distinct origins by long-distance colonisation processes was at the origin of peculiar and unexpectedly rich biological assemblies.

(5) Biodiversity corridors have been proposed for coastal regions, central mountains, and the Nile river (Dumont, 1982; Drake *et al.*, 2011), but studies incorporating modern phylogenetic/phylogeographic analyses are needed to test biogeographic hypotheses and to date diversification events and phylogeographic splits. It is also necessary to investigate diversity in low- and high-dispersal taxa along putative corridors.

(6) Metapopulation systems of biodiversity hotspots associated with micro-scale humid habitats have been detected (e.g. Trape, 2009; Brito *et al.*, 2011*c*; Campos *et al.*, 2012), but it is unknown how landscape features link to gene flow and connectivity, and how climate change may affect such dynamics. Monitoring of climate-change effects should be prioritised in sensitive areas by focusing on water-restricted fauna.

(7) Ecological adaptation and possible hybridisation in contact zones between full species has been suggested (Crochet *et al.*, 2003), but the role of climate and landscape features in defining the extent of ranges, connectivity and gene flow are unknown. Integrative landscape models are needed to understand contact-zone and gene-flow dynamics in desert environments and to strengthen knowledge on evolutionary and adaptation mechanisms to extreme arid conditions.

(8) Present regional red-listing of biodiversity is very limited [amphibians and reptiles of Morocco (Pleguezuelos *et al.*, 2010)] and is urgently needed to be extended to other taxonomic groups and countries to identify threatened biodiversity and define conservation priorities.

(9) Assessments of genetic diversity in captive and semi-captive threatened ungulates have stressed the importance

of using molecular markers for optimising management options (e.g. Godinho *et al.*, 2012), but such assessments are now needed for wild populations, particularly for the identification of management units and effective population sizes and their trends (Crandall *et al.*, 2000). Non-invasive genetic sampling techniques should be prioritised given their usefulness in studying secretive or hard-to-sample species.

(10) Optimised conservation solutions for the Sahara-Sahel biodiversity are lacking. Reserve design solutions targeting biodiversity representativeness and persistence together with human development, are needed. Special emphasis should be given to mitigate expected negative impacts of climate change, incorporating evolutionary processes in conservation solutions, and identifying potential corridors among conservation areas.

VI. CONCLUSIONS

(1) The Sahara-Sahel system is a good model to investigate the effects of extreme climate shifts on biodiversity dynamics. The region is environmentally heterogeneous and has been subjected to profound climatic oscillations that have shaped biodiversity distribution. Biodiversity hotspots and cryptic diversity have been found in restricted and small-sized water-features located in mountains. The system of mountains surrounded by sand seas provides isolated areas to assess responses of species to climatic oscillations. It is an ideal laboratory to study phenology, physiology, tolerance and adaptation to climate change. Patterns currently observed may provide indications on potential outcomes of global warming and increasing aridity that are of particular relevance for neighbouring global biodiversity hotspots, such as the Mediterranean Basin and the West African Forests.

(2) Increasing scientific studies based on modern geomatic and molecular tools, and broad sampling of taxa in these regions, are allowing insights on patterns of biodiversity distribution and evolution. The steep increase in taxonomic research on vertebrates during the last decade suggest that the Sahara-Sahel still harbours cryptic biodiversity in urgent need of research and that biodiversity conservation targets are far from being achieved.

(3) The onset of the Sahara has been associated with diversification processes, mostly for low-mobility vertebrates. Phylogeographic patterns highlight the importance of allopatric divergence in the Sahara-Sahel.

(4) Regional insecurity is growing and the escalating conflict in the Sahel, apart from the associated local human tragedy, is hampering biodiversity research and conservation. The trend of research effort increase experienced in the last decade is thus uncertain for the future. Research priorities and conservation policies can only be achieved fully with the complementary advanced training of local human resources, technology transfer, and improvement of social conditions. Such developments will clearly contribute to the stabilisation of the region and ultimately to conserving biodiversity.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Distribution of species richness of endemic and relict taxa of dragonflies, fishes, amphibians, reptiles, and mammals in hypothesised dispersal corridors and refugia of the Sahara-Sahel region.

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